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BEARING ON HEREDITY AND VARIATION

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NON-RANDOM CROSSING OVER IN THE SECOND CHROMOSOME OF NEUROSPORA CRASSA[1]

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University of Southern California, Los Angeles

Received August 18, 1938

INTRODUCTION

CYTOLOGICAL analysis (LINDEGREN and RUMANN, in press) has shown that *Neurospora crassa* probably contains nine chromosomes. These chromosomes were found to contain respectively, 29, 18, 13, 9, 5, 3, 3, 2, and 1 chromomeres; but since they were not completely uncoiled, the number of ultimate chromomeres is probably at least twice as great. They are certainly the smallest chromosomes in which crossing over has ever been analyzed. The sex chromosome in Drosophila, in which comparable studies have been made, contains at least twenty times more chromomeres. In Neurospora, one linkage group containing six loci has already been established (LINDEGREN 1936). If mutations occur at random, about 35 percent of the mutants should be found in the first chromosome and it seems probable that the sex chromosome, which is the longest genetically, corresponds to the longest cytological chromosome.

The present paper reports a second linkage group containing four loci. The second longest chromosome contains 22 percent of the chromomeres and probably contains the genes of this second linkage group. About half of the genes should be distributed among seven other linkage groups and many other mutants which have not yet been mapped are being carried in stock. None of these has been found to be linked in those tests which were made. All the mutants used in these studies appeared spontaneously.

EXPERIMENTAL

Four loci located in the second chromosome are the spindle fiber attachment (SFA), peach (*Pe*), tuft (*Tu*), fluffy (*F*). Peach (LINDEGREN 1936) differs from normal in its lighter color. The conidia in tuft are clustered together in large bunches. It grows slightly slower than normal. The color of the mature culture is considerably lighter than normal. The conidiophores grow to nearly the same height as normal, but the lower part of the aerial growth is almost white and the conidia are mostly borne at the top in masses separated irregularly from each other by relatively large "moth-eaten" open spaces. Fluffy is a non-conidial mutant, and has already been reported (LINDEGREN 1933).

The genes differentiating these mutants are all distributed in the same

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arm of the second chromosome. Peach is 11.3, tuft is 19.8, and fluffy is 38.7 units from the spindle fiber attachment. It has already been shown that neither peach nor fluffy are in the sex chromosome. A preliminary cross of peach by fluffy indicated that these two genes are linked. A second cross of tuft by fluffy indicated that tuft was also in this linkage group. Tuft, (like peach and fluffy) was shown to segregate independently of the sex differentiating genes. The exact relationships were established by three different crosses, namely, *PeF*×*Tu*, *PeTu*×*F*, and *TuF*×*Pe*. In table I, 278 asci from these crosses are analyzed.

In measuring distances between different loci, advantage is taken of the fact that the arrangement of the spores in the ascus makes it possible to distinguish asci in which the gene pairs were segregated from each other at the first reduction division from those in which second-division segregation occurred. This makes it possible to determine the amount of recombination occurring between the SFA and other loci. For example, in calculating the distance of peach from the SFA, the total number of exchanges in region I is determined and this number is divided by the total number of chromatids. There were 34 asci in which an exchange occurred in region I, but in neither of the other regions. In each exchange two of the four strands interchange; in the 34 asci, 68 of the 136 strands crossed over. The exchanges involving region I (either in I only, or in one or more of the other regions as well) are listed below with the number of crossover chromatids which each contribute to the total number in region I.

Region	*Asci*	*Crossover chromatids*
I	34	68
I & II	5	10
I & III	9	18
I & II	6	12
I & III	6	12
I & II & III	3	6
		126

Since each ascus produces four chromatids; the total number of chromatids is 4 times the total number of asci (278×4=1,112). To obtain the distance of peach from SFA, 126 is divided by 1,112 which equals 11.3. In the same way the total number of crossover chromatids in the other two regions is determined and the distances evaluated (table I).

If no exchange occurs, the heterozygous tetrad in the first reduction division separates into two homozygous dyads, each held together by the SFA (fig. 1). When the SFA splits at the second division, each pair of homozygous chromosomes is separated, but the narrow ascus prevents overlapping of the spindles. Four homozygous chromosomes are formed into nu-

clei in the upper half of the ascus and the four oppositely homozygous chromosomes (containing the corresponding alleles) are lined up in the lower half. Thus no exchange results in a first-division segregation of all the alleles in the chromosome. Since the tetrads are oriented at random on the spindle, there are two possible arrangements of the spores in these *no exchange* asci, either 1 to 4 are A B C and 5 to 8 are a b c, or 1 to 4 are a b c, and 5 to 8 are A B C.

TABLE 1

Classification of type of exchange and calculation of number of crossover chromatids.

			CROSSOVER CHROMATIDS		
			REGIONS		
			I	II	III
No Exchanges		104			
One-Region Exchange in I		34	68	0	0
One-Region Exchange in II		26	0	52	0
One-Region Exchange in III		76	0	0	152
Two-Region Exchanges	2-Strand I & II	5	10	10	0
	2-Strand II & III	2	0	4	4
	2-Strand I & III	9	18	0	18
	3-Strand I & II	6	12	12	0
	3-Strand II & III	3	0	6	6
	3-Strand I & III	6	12	0	12
	4-Strand II & III	2	0	4	4
One-Region	4-Strand III	2	0	0	8
Three-Region Exchanges	2-Strand, 2-Strand	1	2	2	2
	3-Strand, 2-Strand	2	4	4	4
			126	94	210

If an exchange occurs in the first region, there is no recombination of characters, but the dyads on the second spindle are heterozygous instead of homozygous. In the second division each of the heterozygous dyads is split to form two homozygous chromatids. These are then arranged alternately in the ascus in one of the four arrangements shown in figure 2, as a result of the random orientation of the spindles in the two divisions. Similarly a single exchange in region II results in producing four genotypes and there are eight different possible arrangements of the recombined genotypes in the ascus. A study of figure 2 shows several of the other possible arrangements.

The distance of peach from the SFA (11.3 units) indicates that in 22.7 percent of the asci, a single exchange has occurred in region I, similarly the distance of 8.5 between peach and tuft, indicates that in 17.0 percent

of the asci, a single exchange has occurred between peach and tuft. The product .227×.170=.039 gives the fraction of asci in which a simultaneous exchange in both regions may be expected. Therefore, in about 3.9 percent, or 11 of the 278 asci, it would be expected that simultaneous exchanges in regions I and II would be found. The observed number was 14.

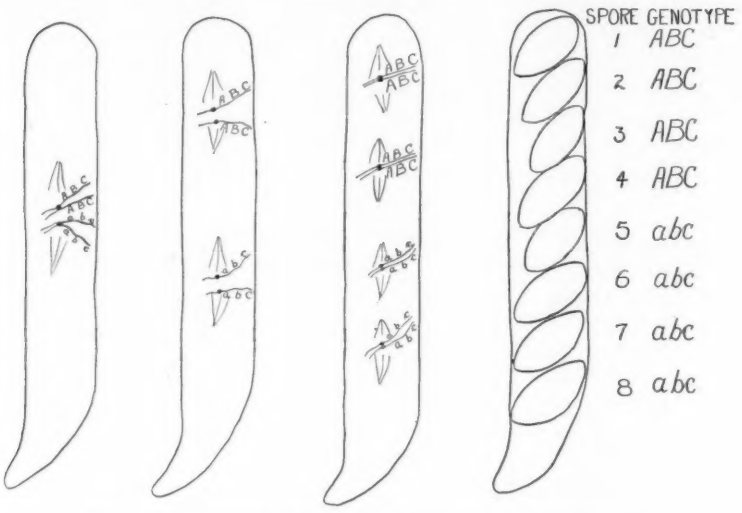

FIGURE 1.—Orientation of spores in the ascus when no exchange occurs.

Comparison of the numbers of calculated and observed exchanges is shown below:

Region	*Calculated*	*Observed*
I & II	11	14
I & III	24	18
II & III	18	10

These data show a deficiency rather than an excess of the number of expected multiple exchanges. An excess of multiple exchanges was found in a study of crossing over in the sex chromosome. However, an examination of the data on the sex chromosome show that this excess only occurs between regions symmetrically placed on opposite sides of the spindle fiber attachment. When regions on one side of the SFA are considered there was not an excess but a deficiency. Thus the present data are in agreement with those already reported. If regions on both sides of the SFA had been studied, it is probable that an excess of multiple exchanges would have been found in the second chromosome also.

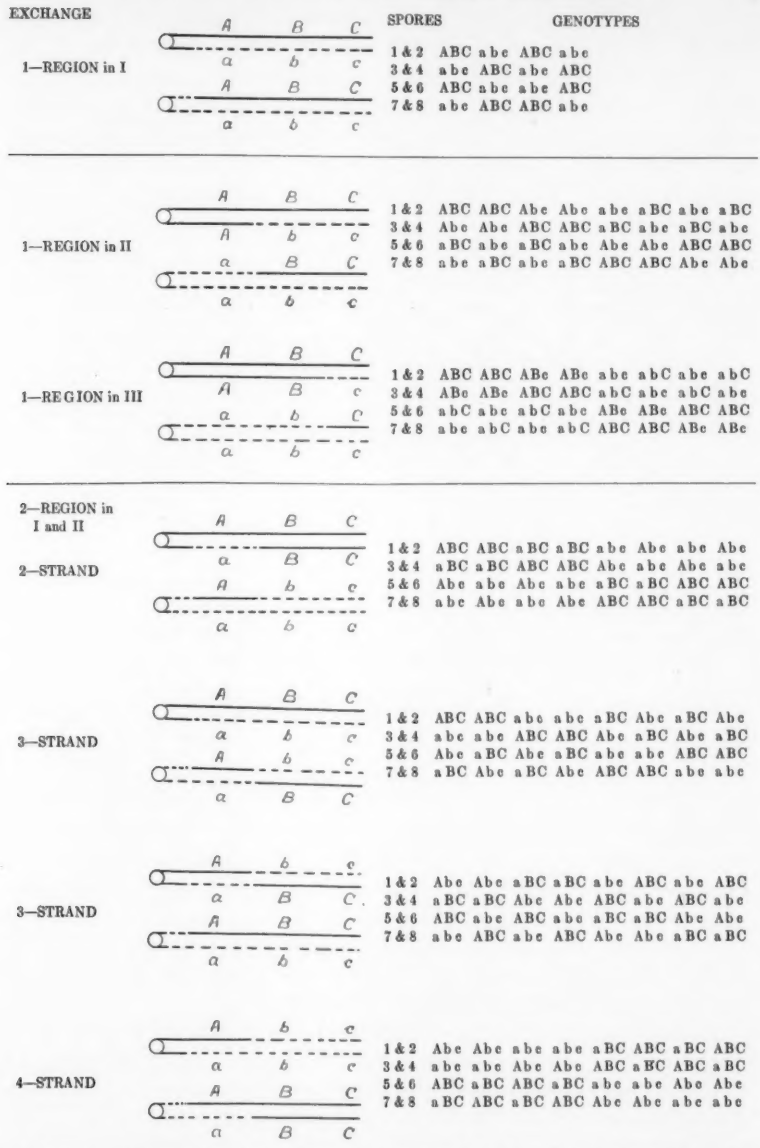
EXCHANGE
SPORES
GENOTYPES
1—REGION in I
1&2 ABC abc ABC abc
3&4 abc ABC abc ABC
5&6 ABC abc abc ABC
7&8 abc ABC ABC abc
1—REGION in II
1&2 ABC ABC Abc Abc abc aBC abc aBC
3&4 Abc Abc ABC ABC aBC abc aBC abc
5&6 aBC abc aBC abc Abc Abc ABC ABC
7&8 abc aBC abc aBC ABC ABC Abc Abc
1—REGION in III
1&2 ABC ABC ABc ABc abc abC abc abC
3&4 ABc ABc ABC ABC abC abc abC abc
5&6 abC abc abC abc ABc ABc ABC ABC
7&8 abc abC abc abC ABC ABC ABc ABc
2—REGION in I and II
2—STRAND
1&2 ABC ABC aBC aBC abc Abc abc Abc
3&4 aBC aBC ABC ABC Abc abc Abc abc
5&6 Abc abc Abc abc aBC aBC ABC ABC
7&8 abc Abc abc Abc ABC ABC aBC aBC
3—STRAND
1&2 ABC ABC abc abc aBC Abc aBC Abc
3&4 abc abc ABC ABC Abc aBC Abc aBC
5&6 Abc aBC Abc aBC abc abc ABC ABC
7&8 aBC Abc aBC Abc ABC ABC abc abc
3—STRAND
1&2 Abc Abc aBC aBC abc ABC abc ABC
3&4 aBC aBC Abc Abc ABC abc ABC abc
5&6 ABC abc ABC abc aBC aBC Abc Abc
7&8 abc ABC abc ABC Abc Abc aBC aBC
4—STRAND
1&2 Abc Abc abc abc aBC ABC aBC ABC
3&4 abc abc Abc Abc ABC aBC ABC aBC
5&6 ABC aBC ABC aBC abc abc Abc Abc
7&8 aBC ABC aBC ABC Abc Abc abc abc

FIGURE 2.—Diagram showing orientation of genotypes in the ascus due to various types of exchanges. Loci *Pe/pe*, *Tu/tu*, and *F/f* are indicated by *A/a*, *B/b*, and *C/c*. The SFA indicated in the diagram is not recognizable in the genotypes, but first division segregation of the SFA means that chromatids in spores 1 to 4 contain SFA's of similar origin, as compared to those in spores 5 to 8.

It is not possible in this study of four-strand crossing over to determine which two of the four strands are involved in any given exchange. In the diagram, the first exchange is arbitrarily designated as always occurring between strands 2 and 3 (fig. 2) actually there are three other possibilities, namely, 1 and 3, 2 and 4, 1 and 4. If this first exchange is followed by a second exchange in another region, the ascus is classified as a two-region exchange ascus. If this second exchange involves the same two strands as the first, that is, strands 2 and 3, this ascus is called a 2-region, 2-strand, ascus,

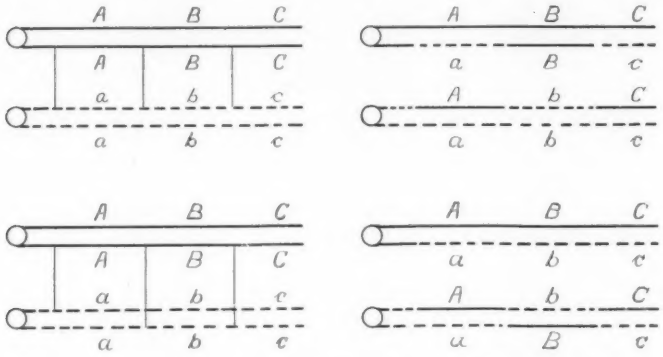

FIGURE 3.—Chromatids produced by the 3-region exchanges. The first is a 2-strand, 2-strand; the second is a 3-strand, 2-strand multiple exchange.

because only 2 of the 4 strands (2 and 3) have participated in the exchanges. Strands 1 and 4 have not been involved in any exchange at all. If the second exchange involves 1 and 4, then the ascus exchange is called a 2-region, 4-strand ascus because all 4 strands, 1, 2, 3, and 4, are crossover strands. Strand 2 crossed over with 3; and strand 1 crossed over with 4. There are two possible kinds of 2-region, 3-strand exchanges: (1) those in which the exchange between strands 2 and 3 is followed in the second region by an exchange between strand 2 and 4; (2) those in which the original exchange between strands 2 and 3 is followed by an exchange between strands 1 and 3. In the former case, strand 1 is a non-crossover strand and in the latter case, strand 4 is a non-crossover strand.

If the second crossover occurs at random with respect to the first, then the four different types of 2-region exchanges shown in figure 2 will occur in equal numbers. That is, the ratio of 2-strand to 3-strand to 4-strand exchanges should be 25 to 50 to 25. In the present paper, there are reported sixteen 2-strand, fifteen 3-strand, and two 4-strand, two-region exchanges. There are three 3-region exchanges, one a double 2-strand as shown in figure 3, the other two were 3-strand, 2-strand exchanges as

shown in the same figure. Therefore, the total ratio of 2-, to 3-, to 4-strand exchanges is 20 to 17 to 4 in the second chromosome. LINDEGREN and LINDEGREN (1937) reported a ratio of 27 to 14 to 8 in the sex chromosome, which is statistically equivalent to the present ratio. Thus, of a total of 90 double exchanges, the ratio is 52 to 34 to 13 and in striking agreement in the two different chromosomes.

In the earlier study the regions were short so that practically no undetected exchanges could have occurred. In the present study, there may have been about ten undetected multiple exchanges in the long region between tuft and fluffy. If a 2-strand multiple exchange occurred in this region it would be undetected. Therefore, although the number of 2-strand exchanges are in excess of those expected, this long region reduces rather than increases their apparent number. A 3-strand exchange occurring within this long region would appear to be a single crossover and would be recorded as such. The 4-strand exchanges can be detected even if they occur in a single region, because each one of the four strands is a crossover. Therefore, the deficiency of 4-strand exchanges like the excess of the 2-strand exchanges is real and not the result of using data involving one long region.

SUMMARY

The discovery of non-random crossing over in the second chromosome, essentially conforming to the type of non-randomness reported in the first chromosome, offers further support to the modification of Belling's theory of crossing over already suggested by the writers.

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THE INTERACTION OF SOME WING MUTANTS IN DROSOPHILA MELANOGASTER

EMANUEL WALETZKY
University of Wisconsin, Madison, Wisconsin

Received August 22, 1938

INTRODUCTION

THE combination effects of many gene mutations in Drosophila seem to be cumulative and roughly proportional to the effect of each single gene. "Disproportionate" combination effects have also been described qualitatively by BRIDGES (1919), BRIDGES and MOHR (1919), LEBEDEFF (1935), and others.

The discovery that two well known sex-linked genes of *Drosophila melanogaster*, bifid and Beadex, produce a striking disproportionate combination effect on wing shape and size permitted a quantitative study of this phenomenon.

MATERIALS

Bifid, symbol *bi*, influences the venation of the wing. All the longitudinal veins are fused at the base of the wing, and the fourth longitudinal vein may fail to reach the margin. A notch may be present in the margin of the wing. The latter feature is very rarely present in the bifid stocks used in this experiment.

Beadex, symbol *Bx*, is represented by a multiple allelic series producing scalloped wings of approximately normal length. The alleles used, in ascending order, are: Bx^r, Bx^1, Bx^2, Bx^3, and Bx^J.

EXPERIMENTAL

A single male with aberrant wings was found by PROFESSOR VICTOR JOLLOS in a culture which had been kept on Pike's Peak. This male was mated to Bx^J females. In the F_2, a number of males with very short, scalloped wings appeared. This new "small wing" type was given to the author for analysis.

It was found that the "small wing" type contained bifid and Beadex-J. Linkage data indicated that the interaction of these two factors produced "small wings." On this view, the original aberrant parental male was bifid. Crossing over produced the F_2 bifid Beadex-J, small wing, males.

This was confirmed by using an unrelated stock of bifid containing the mutant ruby eyes. The loci of bifid, ruby, and Beadex on the X chromosome are 6.9, 7.5, and 59.4, respectively. A bifid ruby female was crossed with a Beadex-J male. All the F_2 crossovers that were ruby and Beadex-J were also bifid and "small wing," if one omits the rare double crossovers. Similar results were also obtained when bifid flies extracted from

a bifid cut-6 garnet-2 bobbed stock were crossed with a Beadex-2 stock.

The interaction of bifid with different Beadex alleles was tested by crossing bifid ruby females to Bx^r, Bx^1, Bx^2, and Bx^3 males, respectively. The three F_1 and the three F_2 cultures made for each Bx allele yielded identical results. F_1 females heterozygous for Bx^r or Bx^1 were phenotypically normal, although only Bx^r is ordinarily recessive. The bifid ruby stock must contain modifiers suppressing the dominance of Bx^1.

Two types of scalloped wings were present in the F_2 males of all four series, and in the females of the Bx^2 and the Bx^3 series: a Beadex type, and a non-Beadex type. Bifid venation was invariably absent in the former, and invariably present in the latter. All the scalloped wing F_2 females of the Bx^r and the Bx^1 series were bifid and non-Beadex in type. Since the corresponding F_1 females had normal wings, Bx^r and Bx^1 are at least incompletely dominant in the presence of homozygous bifid. All the other Beadex alleles tested are dominant. However, all bifid Beadex wings are progressively smaller in the following order: heterozygous Beadex female, homozygous Beadex female, Beadex male.

The accompanying photographs illustrate the difference between the different types of wings in the male. In the Beadex wing, the scalloping is roughly parallel to the long axis. The posterior margin of the wing is always more scalloped than the anterior costal margin, which is frequently normal in the less extreme alleles (figures 1–5).

The bifid Beadex wing is highly variable in shape and size. This made a qualitative comparison of bifid wings containing different Beadex alleles impossible. The scalloping is oblique to the long axis. Both the posterior and the costal margins are equally scalloped at the distal end. In contrast to Beadex, both length and width are greatly reduced.

Large vesicles are frequently formed in Beadex and in bifid Beadex wings during their expansion. Such wings become very crumpled and reduced in length, and have been disregarded in this study.

A qualitatively new type of wing has been produced by the crosses of three different bifid stocks with five different Beadex alleles. It is difficult to see how this disproportionate combination effect could result merely from the summation of the known effects of bifid and Beadex. Quantitative data should permit a decision concerning this point.

Such data were obtained from a single pair mating of a bifid ruby female with a Beadex-1 male, and a bifid ruby female with a Beadex-3 male. The parental stocks were inbred, and all cultures were kept in the same incubator at 25°C. The wings were removed from the F_2 males appearing during the first six days of the culture, and mounted on slides.

All measurements were taken from camera lucida drawings made at a magnification of 47.6 times. Length measurements were taken to a tenth

of a millimeter with an error of less than 0.2 millimeters. Wing areas were measured with a planimeter set so that 25 square centimeters equalled 0.261 planimeter units. The error was small since ten measurements of a normal wing gave a mean of 0.332 with a standard deviation of 0.0017.

Distal length was measured as a straight line connecting the end of the third longitudinal vein with the intersection of the fourth longitudinal vein by the posterior crossvein. The continuation of this line to the proximal margin gave the proximal length. Total length represents the

TABLE 1

Bx³ Series. Means and Standard Errors.

CLASS	AREA	TOTAL LENGTH MM	DISTAL LENGTH MM	PROXIMAL LENGTH MM	CROSSVEIN INTERVAL MM
+	0.2887*	81.89	45.85	36.01	17.45
	±(0.0031)**	(0.51)	(0.32)	(0.33)	(0.19)
bi	0.2765	80.59	44.39	36.09	16.81
	±(0.0032)	(0.54)	(0.38)	(0.36)	(0.18)
Bx^3	0.2497	86.37	51.05	35.17	16.13
	±(0.0039)	(0.61)	(0.41)	(0.38)	(0.20)
bi Bx^3	0.1539	65.81	38.19	27.51	11.74
	±(0.0034)	(1.40)	(1.04)	(0.43)	(0.18)

* The mean of 50 wings.

** The standard error of this mean.

sum of proximal and distal lengths. The crossvein interval was measured on the fourth longitudinal vein. The area measured represents the wing surface distal to a perpendicular line intersecting the first costal break. No width measurements were attempted, since width is so variable in the individual bifid Beadex wing.

The means and standard errors of the measurements are given in tables 1 and 3. All values are based on fifty wings. Tables 2 and 4 give the quotients of the differences between means divided by the standard errors of the differences. The fourth difference tested is that between the experimental value of bifid Beadex and the value which would result from a summation of the effects of bifid and Beadex. Thus, in table 1, the sum

EXPLANATION OF FIGURES 1–5

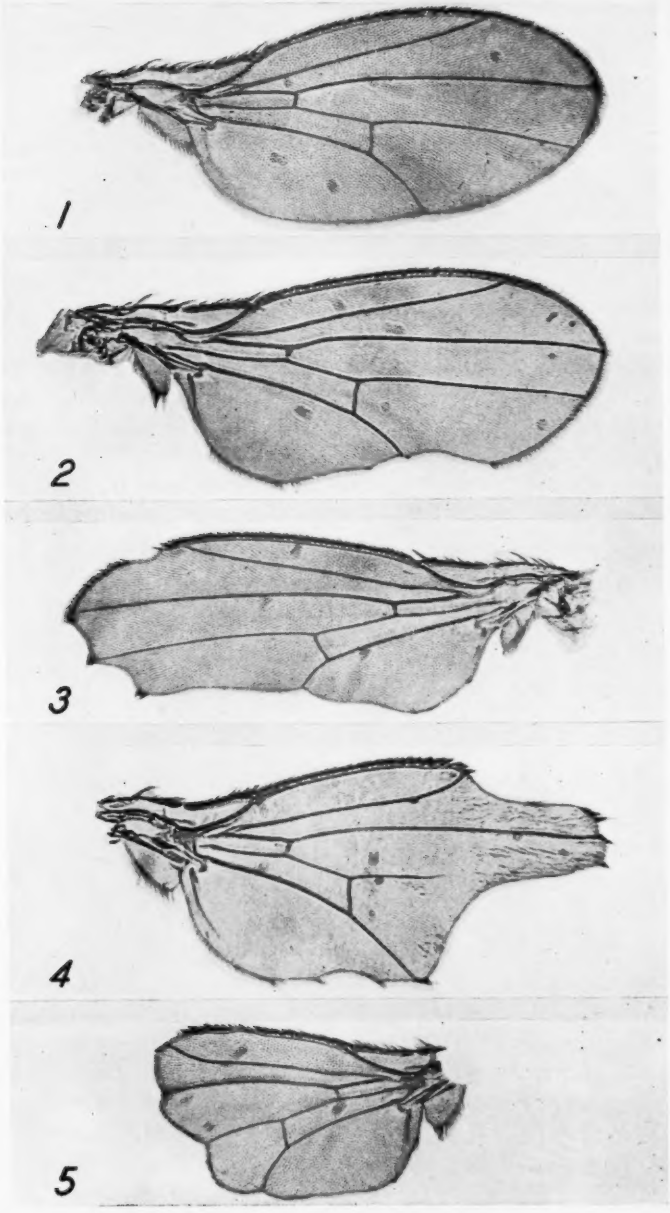
FIGURE 1.—Bifid. ×42

FIGURE 2.—Beadex¹. ×42

FIGURE 3.—Beadex³. ×42

FIGURE 4.—Bifid Beadex¹. ×42

FIGURE 5.—Bifid Beadex³. ×42



FIGURES 1–5. (See opposite page for description.)

TABLE 2

Bx^3 Series. Difference/Error.

DIFFERENCE	AREA	TOTAL LENGTH	DISTAL LENGTH	PROXIMAL LENGTH	CROSSVEIN INTERVAL
+−bi	2.7	1.8	2.9	0.2	2.5
+−Bx^3	7.8	5.7	10.0	1.7	4.7
+−bi Bx^3	29.2	10.8	7.0	15.7	22.0
Additive*	10.3	10.5	8.8	8.7	8.1

* The sum of the first two differences minus the third difference.

of the differences in area of bifid and Beadex-3 from normal is equal to 0.0122 plus 0.0390 or 0.0512. The experimental difference between bifid Beadex-3 and normal is 0.1348. The difference between 0.0512 and 0.1348 is 0.0836. Table 2 shows that this difference is 10.3 times its error.

The measurements of the mutants differ significantly from normal in the following respects: The area and distal length of bifid are smaller. The crossvein interval and the area of Bx^3 are smaller, while the total and distal length are larger. In Bx^1, all the measurements except distal length are smaller. *Bi* Bx^3 and *bi* Bx^1 are smaller than normal in all respects.

TABLE 3

Bx^1 Series. Means and Standard Errors.

CLASS	AREA	TOTAL LENGTH MM	DISTAL LENGTH MM	PROXIMAL LENGTH MM	CROSSVEIN INTERVAL MM
+	0.3290 ±(0.0026)	85.87 (0.45)	47.53 (0.28)	38.31 (0.29)	18.31 (0.18)
bi	0.2973 ±(0.0025)	81.34 (0.40)	44.04 (0.31)	37.31 (0.22)	16.63 (0.10)
Bx^1	0.2939 ±(0.0022)	83.37 (0.29)	47.58 (0.22)	35.85 (0.23)	16.41 (0.16)
bi Bx^1	0.2323 ±(0.0027)	75.09 (0.72)	43.34 (0.54)	31.85 (0.36)	13.68 (0.16)

All the values of *bi* Bx^3 are significantly smaller than those expected from a simple additive effect of bifid and Beadex-3. This is also true in the *bi* Bx^1 wings in regard to area, total and proximal length, and possibly the crossvein interval. The values for *bi* Bx^3 are lower than those for *bi* Bx^1 in all cases. Thus, the areas of the *bi* Bx^3 and the *bi* Bx^1 wings are respectively 53.3 percent and 70.6 percent of the normal wing area. However, none of the differences are statistically significant with the numbers available.

There are also other features of the bifid Beadex wing which cannot be explained by a simple additive effect of bifid and Beadex. In the Bx^1 series, only 12 out of 71 Bx^1 wings had scalloped costal margins, while all 63 *bi* Bx^1 wings had scalloped costal margins. A similar difference was present in the venation of bifid and bifid Beadex wings in both series. In bifid wings, the fourth longitudinal vein failed to reach the margin in 4 out of 167 wings (2.4 percent). This characteristic feature of bifid was observed in 121 out of 179 bifid Beadex wings (67.6 percent), although the other classes of F_2 wings were normal in this respect. The failure of the fifth longitudinal vein to reach the margin in Beadex wings remained unaltered in bifid Beadex wings.

TABLE 4

Bx^1 Series. Difference/Error.

DIFFERENCE	AREA	TOTAL LENGTH	DISTAL LENGTH	PROXIMAL LENGTH	CROSSVEIN INTERVAL
$+-bi$	8.8	7.5	8.3	2.8	8.0
$+-Bx^1$	10.4	4.7	0.1	6.6	7.9
$+-bi\ Bx^1$	25.6	12.7	6.9	14.0	19.3
Additive	4.8	3.2	0.9	4.3	2.6

Less extensive tests of the interaction of bifid with other sex-linked genes producing scalloped wings were made. The mutants cut-6 and scalloped were used. Qualitative examination revealed no difference between cut-6 and bifid cut-6 male wings. The bifid scalloped combination is more difficult to evaluate qualitatively, since scalloped itself is extremely variable. On the whole, bifid scalloped male wings seemed to be more reduced than scalloped wings.

The disproportionate interaction of bifid with scalloped is not as striking as that of bifid with Beadex, in regard to size and shape of the wing. The results of this combination on venation, however, parallel those of the latter. It was found that 0, 8.7, 15.7, and 83.3 percent respectively, of the normal, the bifid, the scalloped, and the bifid scalloped wings had the fourth longitudinal vein interrupted, in a total of 336 wings.

DISCUSSION

GOLDSCHMIDT (1935) has studied the development of Beadex, cut, and other mutants producing scalloped wings. He found that their development was characterized by peripheral degeneration. Our data indicate that other factors are also involved in producing the characteristic dimensions of Beadex and bifid Beadex wings.

The crossvein interval region is not affected by scalloping, nor presumably by peripheral degeneration. It is, however, considerably reduced

in Beadex and bifid Beadex wings. The factors responsible for this decrease do not seem to influence the distal length. Thus, in Bx^3 wings, the distal length, and consequently the total length, are greater than normal. In bifid Beadex wings, the crossvein interval is proportionately more reduced than the distal length.

The interaction of bifid and Beadex seems to be fairly specific. The combinations of other wing mutants with Beadex, reported by CSIK (1934), do not have disproportionate effects. The bifid cut-6 combination effect is also not disproportionate. The description of the original bifid stock by MORGAN and BRIDGES (1915) and the results of the bifid scalloped combination indicate that bifid may act disproportionately with other genes besides Beadex.

The methodological usefulness of disproportionate effects is necessarily limited. The type of interaction with bifid may, however, serve to differentiate between wing mutants whose development and phenotypes are similar, such as Beadex and cut-6.

The author is indebted to PROFESSOR V. JOLLOS for his encouragement and his advice in the preparation of this paper.

SUMMARY

1. Combinations of bifid with five different Beadex alleles produce a qualitatively new type of reduced wing.

2. This disproportionate combination effect is quantitatively much greater than a simple summation of the independent effects of bifid and Beadex.

3. Bifid also interacts disproportionately with scalloped, but not with cut-6.

4. Peripheral degeneration cannot be the only aberrant factor involved in the formation of Beadex and bifid Beadex wings.

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STUDIES ON THE BAR SERIES OF DROSOPHILA V. THE EFFECTS OF REDUCED ATMOSPHERIC PRESSURE AND OXYGEN ON FACET NUMBER IN BAR-EYED DROSOPHILA

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THE investigations which have been directed toward a clarification of the kinetics of facet determination in the Bar series of alleles in Drosophila have, heretofore, been concerned largely with the use of temperature as a suitable and easily controlled variable. The manner in which temperature data have been used is clearly set forth in the work of a number of investigators, notably, KRAFKA, 1920; ZELENY, 1923; DRIVER, 1926; 1931; LUCE, 1931; HERSH, 1934; and MARGOLIS, 1935 a and b.

The present paper is the outgrowth of an effort on the part of the author to find other environmental agencies which might be brought to bear upon the problem. The data presented here deal with the effects of reduced atmospheric pressure, and of a pure oxygen atmosphere on the number of facets in the compound eye.

EXPERIMENTAL

The Effect of Reduced Atmospheric Pressure. The stock used in this phase of the work was a very homogeneous Bar stock designated as stock "B" in earlier studies (MARGOLIS 1936). The flies were reared in one by four inch shell vials containing a banana-agar medium (2 percent agar-agar), seeded with a concentrated yeast suspension (1 cake of yeast per 100 cc water).

A one hour egg-laying period was used in the experiments and the vials containing eggs were then segregated into suitable groups for purposes of the experiment. One group of vials was placed in an incubator at 28°C. for the total period of development; the second group was placed in a low pressure chamber adjusted to maintain a pressure of ½ atmosphere (380–400 mm Hg); and the third group of vials was kept at atmospheric pressure very near to the low pressure chamber. The apparatus used for maintaining reduced pressures has been described fully by DUBIN (1934).

Neither the low pressure chamber nor the room in which it was situated was thermostatically controlled. The experiments were therefore designed to maintain the flies at reduced atmospheric pressure only during that period of development prior to the temperature-effective-period, that is, that period during which temperature is capable of affecting facet number. A preliminary determination of the temperature-effective period for facet

formation in the stock used indicated that the period begins during the second half of the egg-larval stage. This is substantially consistent with investigations on other Bar stocks (DRIVER 1931; MARGOLIS 1935b).

During the time that the flies were exposed to reduced pressure a temperature record of both the room and the low pressure chamber was kept. Frequent readings of the room temperature were made daily. In the case of the pressure apparatus it was not possible to take temperature readings while the chamber was in operation. The chamber was therefore opened for a short period daily and the temperature fluctuation for a 24 hour interval was recorded from a maximum-minimum thermometer. Table 1 gives the data on temperature control. The average temperature of the tank for a 24 hour interval was computed simply as the mean between the maximum and the minimum temperature for that 24 hour interval. It is evident that the average temperature calculated in this way may be subject to considerable error although the close approximations of chamber temperature to room temperature indicate that in this case there is probably no great error. The total range of temperature variation in the tank was 14.4° to 19.4° and in the room 15° to 19°.

TABLE 1

Temperature control in pressure experiment.

	AVERAGE ROOM TEMP.	AVERAGE TANK TEMP.
12/6	18.4°	18.1°
12/7	17.6°	16.7°
12/8	16.6°	16.6°
12/9	17.7°	17.5°
12/10	16.3°	16.7°
	17.3°	17.1°

After remaining at reduced pressure for 52, 74, 96, and 120 hours, respectively, groups of vials were transferred from the low pressure chamber to a 28° incubator. At these same times vials containing larvae which had developed at atmospheric pressure near the chamber were transferred to the same incubator to serve as controls. This incubator also contained those flies which had spent their full period of development there.

The data on facet number for the 3 groups of flies are given in table 2. The mean facet numbers for the flies reared at 28° for the total period of development serve as controls for both of the other groups, namely those flies spending a portion of their early development in the reduced pressure chamber before transfer to 28°, and those reared for corresponding periods at room temperature and atmospheric pressure prior to transfer. It is evident that neither of these groups had yet been affected by the lower temperature of the room or pressure chamber.

Our interest, however, centers upon the possible effect of the reduced pressure upon the mean facet numbers. Comparing, group for group, those flies which had spent part of their development at reduced pressure with those flies which had spent equivalent parts of their development at atmospheric pressure, a definite interpretation of the data is difficult. In the males there is evident in each group a small, but possibly significant, decrease in facet number in those flies developing at reduced pressure. When analyzed in terms of significance of differences we find that only in the 120 hour groups is the difference in means statistically significant. In the other three groups the difference in means is in each case less than twice the standard error of the difference.

TABLE 2

Effect of reduced atmospheric pressure on facet number.

HRS. AT ATMOSPHERIC PRESSURE BEFORE TRANSFER TO 28°	HRS. AT REDUCED PRESSURE BEFORE TRANSFER TO 28°	MALES M±S.E.	MALES V PERCENT	MALES N	FEMALES M±S.E.	FEMALES V PERCENT	FEMALES N
	52	66.8±0.68	8.8	75	53.7±0.80	11.4	58
52		68.3±0.76	9.7	75	52.4±0.69	9.6	53
	74	69.9±0.89	10.9	74	51.0±0.66	8.7	45
74		72.4±0.97	11.5	74	53.4±0.62	8.4	53
	96	69 4±1.03	9.5	41	53.6±0.75	8.7	39
96		71.6±1.04	12.4	73	57.0±0.89	10.9	49
	120	66.1±0.81	10.0	67	53.6±0.59	9.6	75
120		72.1±0.96	8.9	45	55.4±0.75	8.0	35
Controls at 28° for total development		71.6±0.82	11.5	104	52.9±0.45	8.3	96

In the females there is a similar but less systematic difference in mean facet numbers of corresponding groups. The flies transferred at 52 hours present the exception in that those which developed at reduced pressure are slightly, but not significantly, larger than the ones which developed at atmospheric pressure. The differences within the 74 and 96 hour groups, respectively, are statistically significant but not in the 120 hour group.

A definite conclusion concerning the effect of reduced atmospheric pressure on facet number is hardly justified beyond pointing out that there is a small but doubtfully significant reduction in number. We shall return to this after considering the effect of a pure oxygen atmosphere on facet number.

One other feature of the data in table 2 requires brief comment. The coefficient of variability for each group is given. In general there is no evidence of a trend in this statistic in groups transferred at successive intervals. This is further confirmation that the flies had not yet entered the temperature-effective period for the character under consideration (MAR-

GOLIS 1935 b; CHILD 1935). Moreover, there is no large or systematic difference between corresponding groups. This shows that the reduced pressure had not affected variability.

The Effect of a Pure Oxygen Atmosphere. The experiments to be discussed here were carried out about a year and a half after the experiments described in the preceding section. The same Bar stock (stock B) was used but this had been inbred for another 20 generations in the interval between experiments. This fact is pointed out since there is evidence of accumulation of modifiers for high facet number during the period of inbreeding. The facet counts in control flies reared at 28°, therefore, show a significant increase in the oxygen experiments.

TABLE 3

Effect of oxygen on facet number.

	MALES			FEMALES		
	M±S.E.	V PERCENT	N	M±S.E.	V PERCENT	N
Controls at 28°	80.7±2.01	12.7	26	57.2±0.91	10.1	40
Flies placed in O_2 at 24 hours age for 48 hours	111.1±3.01	14.3	28	76.6±1.74	11.8	27
Flies placed in O_2 at 48 hours age for 42 hours	101.3±3.42	15.8	22	64.3±1.33	11.0	28

In these experiments small vials of about 2 to 3 cc capacity were used for the development of the larvae. These vials were half-filled with the usual banana-agar medium seeded with a drop of thick yeast suspension. Ten to 15 eggs were placed in each vial which was then covered by two thicknesses of cheesecloth held in place by rubber bands. All vials were then placed in a 28° incubator to begin their development.

After 24 hours of development at 28° under ordinary atmospheric conditions, one group of vials was placed in 8 ounce bottles (one vial per bottle), into which a pure oxygen atmosphere was introduced. These bottles served as oxygen chambers and were immediately placed in the 28° incubator. The larvae were removed from the oxygen chambers after 48 hours and completed their development under ordinary atmospheric conditions at 28°.

The same procedure was followed with a second group of larvae after 48 hours of development under ordinary atmospheric conditions at 28°. This group remained in the oxygen chambers for only 42 hours.

The third group of larvae developed completely under ordinary atmospheric conditions at 28°.

The mean facet counts and coefficients of variability for the 3 groups of flies are given in table 3. The difference in means is clearly evident and statistically significant in both males and females. Flies developing from the 24 hour larvae exposed to oxygen for 48 hours show an increase in facet number over the controls of about 38 percent in the males and 25 percent in the females. Flies developing from the 48 hour larvae exposed to oxygen for 42 hours show an increase in facet number over the controls of about 25 percent in the males and 12 percent in the females.

In respect to the coefficients of variability there appears to be some slight increase in the males exposed to oxygen. This is of doubtful significance when the relative uniformity in the females is considered.

DISCUSSION

The use of temperature in earlier studies has made it possible to single out certain facet forming processes in virtue of their differential temperature characteristics, for example, those facet-forming processes which during a particular developmental period differ from other processes in their response to temperature. This period has been variously designated as the temperature-effective period or sensitive period. In the case of Bar this period falls approximately within the third quarter of egg-larval development, although there is some variation with temperature (DRIVER 1931).

It is evident that other processes determining facet number must occur in the interval between the initiation of development and the beginning of the temperature-effective period. It has not, however, been possible to single out these processes through the use of temperature in Bar. In the wild type, on the other hand, the effect of temperature on facet number extends back into early embryonic stages, possibly to the very beginning of development (MARGOLIS and ROBERTSON 1937).

The data on the effect of oxygen offer clear evidence that processes which determine facet number in Bar are taking place at least as early as the second day of development at 28°, that is, about a day before the beginning of the temperature-effective period. This may be seen by comparing the facet counts of the two groups of flies which were exposed to oxygen and also their periods of exposure. The group placed in oxygen at 24 hours of development showed the greater increase. This could only occur if facet determining processes were taking place some time before 48 hours of development. The time difference between the 48 hour and 42 hour exposures to O_2 is probably of no significance since in the flies exposed for the shorter period puparium formation had already begun, and at this time the ommatidia are established as morphological units whose number is already determined (KRAFKA 1924).

The preliminary character of the foregoing experiments leaves much to

be desired in the way of localizing the period during which oxygen affects facet number, which might be called the oxygen-sensitive period. Moreover, data on the effect of different partial pressures of oxygen would be very desirable.

We may return now to the bearing of the oxygen experiments on the possible significance of the small decrease in facet number brought about by reduced atmospheric pressure. The writer is disposed to the view that the decrease in facet number is real and not merely an error of random sampling. This is based upon the consideration that decreasing the partial pressure of oxygen may be expected to decrease facet number, since an increase in partial pressure resulted in increased facet number. Such an assumption, however, requires reservations since we may be dealing with a threshold phenomenon in which the partial pressure of oxygen, within a limited range, has no effect in altering facet number. Moreover, the pressure and oxygen experiments are not strictly comparable since in the former both the partial pressure of oxygen and total atmospheric pressure are reduced. The present experiments do not permit an assignment of the observed effect to one of these variables rather than the other.

While the data presented here are not adequate for answering many questions which arise, their significance is clear. The use of pressure and oxygen tension as environmental variables presents the possibility of further clarification of the kinetics of facet determination and may be applied to the study of other gene controlled developmental processes.

SUMMARY

Data on the effects of reduced atmospheric pressure and of a pure oxygen atmosphere on the development of facets in Bar-eyed Drosophila are presented.

Flies which had spent varying portions of their egg-larval period (2 to 5 days) at one-half atmosphere pressure showed a very small, but for the most part statistically insignificant decrease in facet number. Exposures to reduced pressure all took place before the beginning of the temperature-effective period.

Flies developed from larvae which had spent from the 24th to the 72nd hour of development in a pure oxygen atmosphere at 28° showed a marked increase in facet number when compared with controls raised under normal atmospheric conditions at 28°. A second group which had spent from the 48th hour of development to the 90th hour in oxygen showed a somewhat smaller but significant increase in facet number.

It is concluded from these results that facet determining processes are in operation before the beginning of the temperature-effective period, that is, about 50 hours at 28°; and that these can best be studied through the

systematic use of new and controllable environmental variables such as the ones used here.

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GENETICS OF NATURAL POPULATIONS. III GENE ARRANGEMENTS IN POPULATIONS OF DROSOPHILA PSEUDOOBSCURA FROM CONTIGUOUS LOCALITIES

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INTRODUCTION

SEVENTEEN gene arrangements, related to each other as single or multiple inversions, were described by DOBZHANSKY and STURTEVANT (1938) in the third chromosome of *Drosophila pseudoobscura*. Some of these gene arrangements have a wide, and others a narrow geographical distribution. In some localities the entire population is uniform, but more commonly several arrangements are found together. Differences between populations may be either qualitative or quantitative. Thus, three gene arrangements (Standard, Arrowhead and Chiricahua) were found in each of the eleven populations from isolated mountain ranges in the Death Valley region, California, studied by DOBZHANSKY and QUEAL (1938). The relative frequencies of these arrangements proved, however, to vary rather widely from range to range, there being no pronounced geographical regularity in these variations. Adjacent ranges do not tend to be more similar than remote ones. Differences of this kind are expected to occur in isolated populations whose effective size is not very large (WRIGHT 1931).

The question arises, however, whether a *D. pseudoobscura* population inhabiting a mountain range may be considered to represent a single breeding unit, or whether it is in turn composed of still smaller colonies whose genetic composition can diverge, within limits, due to the same kind of causes, which provoke the differentiation of larger populations described by DOBZHANSKY and QUEAL (1938). To answer this question, samples of the population of *D. pseudoobscura* were taken in different localities on the same mountain range and the relative frequencies of the different gene arrangements found there were determined. As shown below, significant differences between samples are present, thus proving that some genetic diversification can occur even within an ostensibly continuous population.

MATERIAL AND METHODS

The population of *D. pseudoobscura* inhabiting the Panamint Mountains, California, was selected for the analysis. This mountain range, forming the southwestern boundary of Death Valley, has a maximum elevation

of more than 11,000 feet above sea level; its slopes are crevassed with deep canyons running eastward and westward from the crest. The canyons as well as the crest are covered with a forest-like growth consisting chiefly of piñon (*Pinus monophylla*). This growth begins at an elevation of approximately 6,000 feet, and extends to the base of the highest peaks. *D. pseudoobscura* is encountered in the forested zone and not below it. The population inhabiting Panamint Mountains may be considered isolated from those inhabiting other forested mountains in the same region (cf. DOBZHANSKY and QUEAL 1938).

Samples of flies were collected in seven different canyons on the western slope of the Panamints. The altitude of localities varied from 6,300 to about 8,200 feet (fig. 1), and the distance between them from 4 to 6 miles. It may be noted here that the forest cover is practically continuous on the sides of these canyons, on the ridges separating them, as well as on the main ridge, although the northern exposures have, in general, a denser growth than the southern ones. An especially close connection is found between Jail and Hall canyons; Surprise and Pleasant canyons are somewhat further apart. The geographical and ecological conditions are rather similar everywhere, and there is no apparent impediment for migration of flies from one canyon to others.

Collection in Nemo and Wildrose canyons was made on the 26th and 27th of May, and in the other canyons from the 13th to 20th of June 1938. In most of the cases the flies were separated according to sex in order to avoid matings, and were transported in vials to the laboratory. The methods of determining the structure and the frequency of the various gene arrangements were the same as used by DOBZHANSKY and QUEAL (1938). The females were placed separately in cultures and the salivary gland chromosomes of the larvae were analyzed. Usually one larva was taken from each culture, and its chromosomes were examined. When the number of wild flies from a given locality was insufficient, by analyzing the salivary chromosomes of 10 or more larvae, the chromosome structure of the mother as well as that of the father was assumed to be determined. Wild males were mated to orange purple females, both of which genes are located in the third chromosome which had the Standard gene arrangement. Seven larvae from the F_1 generation were dissected and the gene arrangements in the two paternal third chromosomes inferred from the analysis.

GENE ARRANGEMENTS AND THEIR FREQUENCIES IN THE PANAMINT POPULATIONS

Six previously known gene arrangements have been found in the populations of the canyons, namely: "Standard," "Arrowhead," "Chiricahua," "Santa Cruz," "Tree Line" and "Mammoth" arrangements. Arrowhead

differs from Standard in having one, Chiricahua, Tree Line and Mammoth in having three, and Santa Cruz in having two inversions (DOBZHANSKY

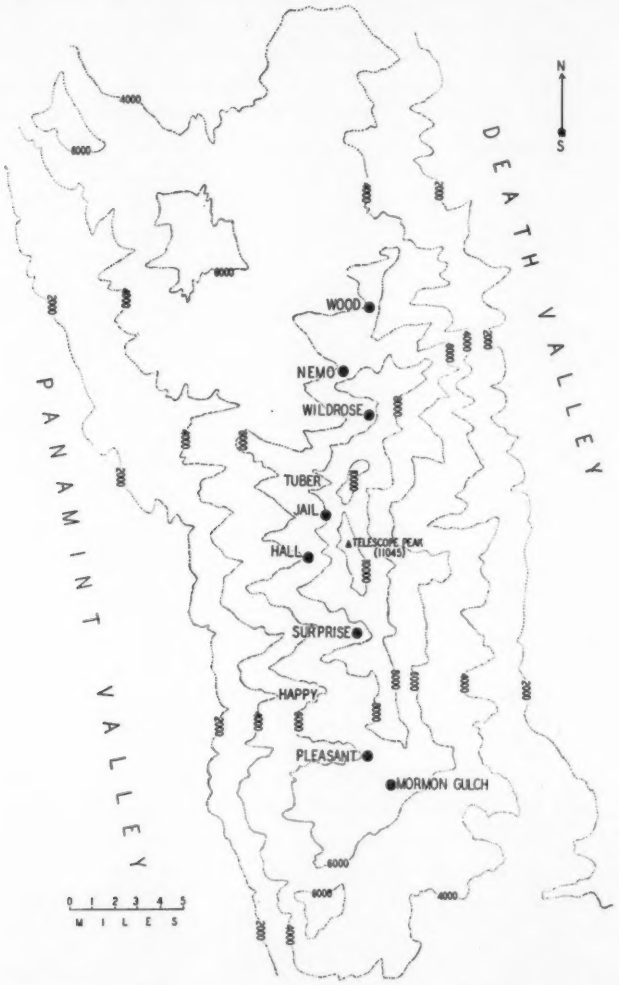

FIGURE 1.—A topographic map of the Panamint Range. Localities in which collection has been made are indicated by circles. (Data from Mormon Gulch are not included in the present paper.)

and STURTEVANT 1938). The distribution and the frequencies of these gene arrangements are given in table 1.

In addition to the six canyons tabulated above, another canyon called Wood Canyon was also explored. It is the northernmost canyon in the Panamint range having tree vegetation. Only one female and two males were trapped. The gene arrangements in the 8 chromosomes (4 from the female, 2 from each male) are as follows: 1 Standard, 6 Arrowhead, and 1 Chiricahua. The small number of chromosomes analyzed prevents us from drawing any conclusions concerning the true genetical constitution of this population.

TABLE 1

Frequencies (in percent) of the six gene arrangements found in different canyons of the Panamint Mountains.

CANYON		STANDARD	ARROWHEAD	CHIRICAHUA	TREE LINE	SANTA CRUZ	MAMMOTH	CHROMOSOMES TESTED
Nemo	♀	48.04±5.38	32.35±4.58	19.61±3.87				102
	♂	25.00±8.83	45.83±3.16	29.17±9.27				24
	total	43.65±4.35	34.92±4.24	21.43±3.60				126
Wildrose	♀	41.43±5.83	30.00±8.36	24.29±5.09		2.86±1.73	1.43±1.49	70
	♂	27.91±4.79	44.19±5.29	25.58±4.69	1.16±1.02	1.16±1.02		86
	total	33.97±3.74	37.82±3.87	25.00±3.46	0.64±0.60	1.92±1.03	0.64±0.60	156
Jail	♀	43.66±3.16	29.92±2.82	21.31±2.44	0.41±0.37			244
	♂	35.71±9.12	50.00±9.43	14.29±6.55				28
	total	47.06±3.00	31.99±2.64	20.59±2.49				272
Hall	♀	37.50±4.12	45.59±4.24	15.50±2.82	4.41±1.73			136
	♂	25.00±9.64	50.00±1.18	25.00±9.64				20
	total	35.90±3.74	46.15±4.00	14.10±2.64	3.85±1.41			156
Surprise	♀	34.68±4.24	44.35±4.35	13.71±3.00	7.26±2.23			124
	♂	42.00±7.59	40.00±6.92	14.00±4.89	4.00±2.64			50
	total	36.78±3.60	43.10±3.71	13.79±2.44	6.32±1.73			174
Pleasant	♀	22.45±4.12	46.94±5.02	30.61±4.58				98
	♂	26.67±4.56	47.78±5.21	20.00±4.18	5.56±2.31			90
	total	24.47±3.07	47.34±3.60	25.53±3.16	2.66±1.17			188
Totals		**37.51±1.48**	**39.74±1.49**	**20.15±1.24**	**2.24±0.45**	**0.28±0.11**	**0.09±0.09**	**1072**

Table 1 shows that the gene arrangements are present in different proportions in different canyons. While the Standard and Arrowhead arrangements have the highest frequencies, Chiricahua is less frequent and the proportion of the three others (Tree Line, Santa Cruz, Mammoth) is probably so small that they were not encountered at all in the populations of some canyons. The frequencies of gene arrangements in the two sexes are given separately, each observed frequency is accompanied by its standard error. There is an apparent difference between the sexes. This difference is especially marked in the population from Wildrose canyon, where the numbers of chromosomes tested in the two sexes are very close. An analysis of variance was made using the BRANDT and SNEDECOR method of test of significance. The χ^2 of the difference between sexes in the various canyons is as follows:

Nemo:	4.202	Hall:	1.468
Wildrose:	4.136	Surprise:	0.832
Jail:	4.684	Pleasant:	0.773

Neither the values of single χ^2 (for 2 degrees of freedom) nor the sum of χ^2 (for 12 d. f.) of the sex-difference in the whole Panamint population are significant.

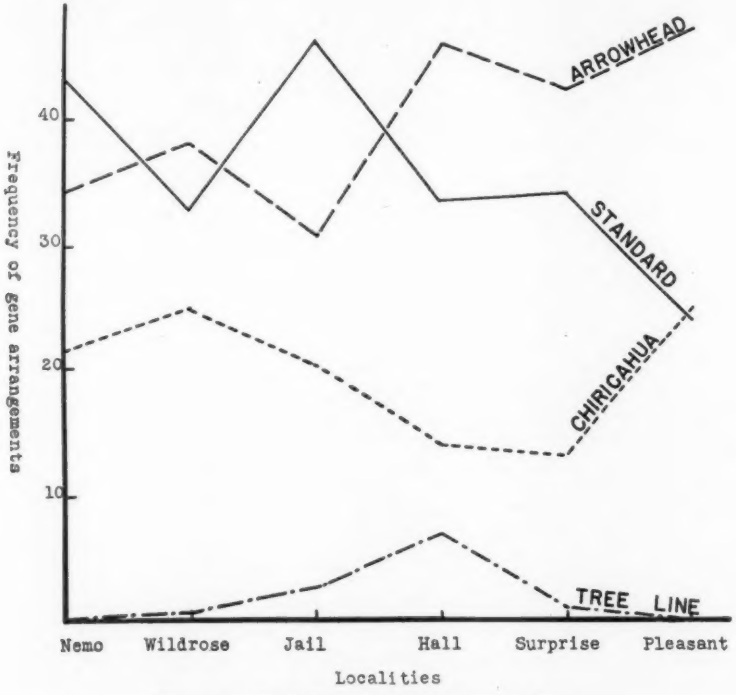

FIGURE 2.—Graph illustrating the frequencies of gene arrangements in the various localities.

Similar statistical analysis was undertaken to determine the significance of the difference with respect to the frequencies of the various gene arrangements observed in the different canyons. The χ^2 value was calculated to be 33.9782. The probability that the difference between canyons is due to chance alone is less than 0.01 for 10 degrees of freedom. The analysis of variance clearly shows that the variations in the frequencies of the same gene arrangements observed in the different localities are very significant. In view of this fact, a question naturally arises: is there a geographical trend in these variations?

TABLE 2

The observed and expected frequencies of inversion homozygotes and heterozygotes in populations of different canyons.

CANYON		STANDARD / STANDARD	ARROWHEAD / ARROWHEAD	CHIRICAHUA / CHIRICAHUA	STANDARD / ARROWHEAD	STANDARD / CHIRICAHUA	ARROWHEAD / CHIRICAHUA
Nemo	obs.	12	7	4	21	10	9
	exp.	*12.00*	*7.46*	*2.89*	*19.20*	*11.79*	*9.43*
Wildrose	obs.	6	11	2	19	19	16
	exp.	*9.00*	*11.15*	*4.87*	*20.04*	*13.24*	*14.75*
Jail	obs.	28	13	6	44	28	16
	exp.	*30.12*	*13.92*	*5.77*	*40.94*	*27.36*	*17.91*
Hall	obs.	10	15	3	28	5	11
	exp.	*10.05*	*16.61*	*1.95*	*25.85*	*7.90*	*10.15*
Surprise	obs.	7	10	1	37	7	14
	exp.	*11.77*	*16.16*	*1.65*	*27.58*	*8.12*	*10.34*
Pleasant	obs.	5	15	4	26	9	30
	exp.	*5.63*	*21.07*	*6.13*	*21.78*	*11.70*	*22.72*
Total	obs.	**68**	**71**	**20**	**175**	**78**	**96**
	exp.	*75.41*	*84.65*	*21.76*	*159.78*	*81.02*	*85.84*

CANYON		STANDARD / SANTA CRUZ	ARROWHEAD / SANTA CRUZ	STANDARD / TREE LINE	ARROWHEAD / TREE LINE	CHIRICAHUA / TREE LINE	ARROWHEAD / MAMMOTH
Nemo	obs.						
	exp.						
Wildrose	obs.	2	1	1			1
	exp.	*1.12*	*1.13*	*0.34*			*0.37*
Jail	obs.				1		
	exp.				*0.32*		
Hall	obs.			3	3		
	exp.			*2.25*	*2.77*		
Surprise	obs.			6	4	1	
	exp.			*4.05*	*4.74*	*1.52*	
Pleasant	obs.			1	3	1	
	exp.			*1.32*	*2.27*	*1.28*	
Total	obs.	**2**	**1**	**11**	**11**	**2**	**1**
	exp.	*1.16*	*1.19*	*9.03*	*9.54*	*4.84*	*0.37*

It is obvious from the data that the Tree Line arrangement is most frequent in the middle region of the Panamint range. While the frequencies of Arrowhead arrangement gradually increase towards the south, the reverse is true for the Standard arrangement (fig. 2). Furthermore, adjacent canyons tend to be more nearly similar than do remote canyons. This is best expressed in populations inhabiting Hall and Surprise canyons.

RANDOMNESS OF MATINGS

The distribution of inversion homo- and heterozygotes in the different canyons is given in table 2.

The observed and expected frequencies agree very well. There is a slight, statistically insignificant excess of heterozygotes. The reverse condition was found by DOBZHANSKY and QUEAL (1938); they observed a small increase in the number of inversion homozygotes.

It was found that females sometimes mate with two or more males in succession. Evidence that double matings may occur in nature was found during the present study. The frequency and structure of the gene arrangements in 10 F_1 larvae of one wild female was found to be as follows: 4 Standard/Arrowhead; 2 Standard/Chiricahua; 2 Arrowhead/Arrowhead and 2 Standard/Standard. According to the first three classes, the genetical constitution of the parents is Standard/Arrowhead×Chiricahua/Arrowhead. Consequently, no larvae of Standard/Standard constitution could be expected in the F_1 generation. The presence of this class is probably due to the fact that the female mated twice, the second male having a chromosome with the Standard gene arrangement.

The other evidence showing that multiple matings occur in nature was obtained when the "sex-ratio" conditions were analyzed in the F_1 generations of wild females. It was reported by STURTEVANT and DOBZHANSKY (1937) that either very few or no sons appeared in the F_1 generation of a female if she was mated to a male carrying "*sr*" ("sex-ratio" gene or genes). Some F_1 cultures of wild females were encountered during the present study in which the proportion of males was found to be between 20–40 per cent. A complete sex-ratio condition in the Panamint strain allows 0–5 per cent of males in the F_1 generation. The greater number of males may have been brought about by a second mating with a normal male.

VARIATIONS IN THE FREQUENCIES OF GENE ARRANGEMENTS FROM YEAR TO YEAR

The frequencies of the various gene arrangements in the population of the Wildrose canyon were determined in 1937 (DOBZHANSKY and QUEAL 1938) and in 1938 (my data). The localities where the collecting was done are almost exactly the same: DOBZHANSKY's trap bottles being spaced

somewhat more widely than mine. The time of collecting was the middle of May in 1937, and the end of the same month in 1938. A comparison of both sets of data is presented in table 3.

TABLE 3

The frequencies of various gene arrangements in Wildrose Canyon on two successive years.

YEAR	STANDARD	ARROWHEAD	CHIRICAHUA	SANTA CRUZ	TREE LINE	MAMMOTH	CHROMOSOMES TESTED
1937	13.83±1.56	67.41±2.11	18.75±1.75				224
1938	33.97±3.74	37.82±3.87	25.00±3.46	1.92±1.03	0.64±0.6	0.64±0.6	156

$\chi^2=33.7512$ D.f.=2 P=<.01

Three gene arrangements, namely Santa Cruz, Tree Line and Mammoth, were detected in 1938, but not in 1937. Santa Cruz and Tree Line are recorded in the Death Valley region for the first time, while Mammoth has been known to occur on other mountain ranges (Lida, Cottonwood) but not on Panamint. The failure to detect these gene arrangements in 1937 may be due either to sampling errors, or to increases of their frequencies in the population. It is highly improbable that they arose there de novo, since spontaneous changes in the gene arrangement are extremely rare; the variations in the gene arrangement in *D. pseudoobscura* described in an earlier paper (KOLLER 1936) were probably present in the experimental strains long before the cytological study was made.

The most important conclusion following from the data presented in table 3 is that the frequencies of the gene arrangements in the same population are not constant from year to year. In 1938 the frequencies of Standard and Chiricahua chromosomes were higher, and of Arrowhead, lower than in 1937. The χ^2 gives the value 33.7572 which is highly significant. Comparable data for the frequencies of the gene arrangements were also obtained for another locality, namely, for the Mount Whitney canyon (Sierra Nevada). Populations of race A and race B of *D. pseudoobscura* were collected in this canyon in mid-July of 1937 (DOBZHANSKY and QUEAL 1938), and again in mid-July of 1938. Table 4 shows the results.

In 1938 two new gene arrangements, namely, Tree Line and Olympic, were found in the Mount Whitney canyon. The frequencies of other gene arrangements underwent no striking changes. To test the statistical significance of the differences observed, the χ^2 values were calculated and proved to be 4.107 for race A and 3.984 for race B respectively. For two degrees of freedom, the P values are between 0.20 and 0.10, hence not significant.

A third set of similar data concerns the population of San Gabriel canyon in 1936 and 1937 (DOBZHANSKY and STURTEVANT 1938). The fol-

lowing frequencies of the various gene arrangements were found in this locality:

Year	Standard	Arrowhead	Chiricahua	Tree Line	Chromosomes tested
1936	14.8	27.8	40.7	16.4	57
1937	57.5	27.7	10.6	4.3	47

Despite the small numbers of the chromosomes tested, the differences are clearly significant: the χ^2 value is 30.3942. The conclusion is justified that pronounced changes in the frequencies of the gene arrangements have taken place in populations inhabiting the Wildrose and San Gabriel canyons, but not in Mount Whitney canyon.

"SEX-RATIO" AND MUTANT GENES

The "sex-ratio" gene is localized in the right limb of the X chromosome, and is associated with a triple inversion. Any male which carries it produces only a few or no sons, owing to the fact that during the spermatogenesis no Y-carrying sperms are formed. The "sex-ratio" gene (*sr*) was found to be widely distributed in free-living populations of *D. pseudoobscura* and other related species (STURTEVANT and DOBZHANSKY 1936). Its frequency in the populations of different canyons of the Panamint range is given below:

CANYONS	NO. OF X CHROMOSOMES WITH "SR"	NO. OF X CHROMOSOMES TESTED	PERCENT OF X CHROMOSOMES WITH "SEX-RATIO"
Nemo	2	11	18.18
Wildrose	10	44	22.73
Jail	7	44	15.9
Hall	0	9	0
Surprise	3	23	13.04
Pleasant	6	44	13.64
Total	28	175	16.00

In 1936, DOBZHANSKY and QUEAL (1938) found that 8.09 percent of the 136 X chromosomes in the Wildrose population tested carried the "sex-ratio" gene.

The populations of the different canyons were tested for the presence of two third-chromosome genes: orange and purple. For this purpose, the wild males were crossed to orange purple females and the F_1 generation was inspected; 596 third chromosomes were thus analyzed, and one chromosome was found to be carrying the gene orange. One half of the F_1

offspring in this culture had the orange eye color. No purple mutant genes were found during the present study.

TABLE 4

The frequencies of various gene arrangements in Mount Whitney Canyon in two successive years.

RACE	YEAR	STANDARD	ARROWHEAD	CHIRICAHUA	TREE LINE	OLYMPIC	WAVONA	KLAMATH	CHROMOSOMES TESTED
A	1937	21.73±6.07	69.57±6.78	8.70±4.16					46
	1938	20.44±4.16	56.50±5.11	18.08±3.92	3.19±1.76	1.06±1.01			94
B	1937	20.30±4.61					78.40±4.75	1.30±1.21	74
	1938	25.71±5.21					67.14±5.61	7.14±3.07	70

For Race A: $\chi^2=4.107$ D.f.=2 P=0.20—0.10
For Race B: $\chi^2=3.984$ D.f.=2 P=0.20—0.10

DISCUSSION

The analysis of the chromosome structure has shown that the population of *D. pseudoobscura* inhabiting the Panamint Mountains is not uniform. Population samples from the different canyons proved to be not alike. The population of the Panamints is differentiated into smaller breeding units having more or less different genetic constitutions. Whether or not the entire population of a canyon may be considered an elementary breeding unit can be decided only by further investigations. Anyway, the subdivision of an inhabited territory (mountain range) into geographical units (canyons) is, in this case, reflected in a corresponding subdivision of the fly population.

No local differentiation can occur in a panmictic population inhabiting a territory of any size. Local colonies which do not interbreed absolutely at random may or may not drift apart in their genetic constitution. Indeed, if the colonies exchange a sufficient number of migrants every generation, a genetic uniformity will continue to prevail. If, however, the migration rate is small, a differentiation is liable to occur. As shown by WRIGHT (1931 and other works), a reduction of the effective size of the breeding population is followed by random fluctuations in the frequencies of the genes (or chromosome structures) present in it. The amplitude of the fluctuations is negatively correlated with population size: the smaller the size the larger the fluctuations.

Since the frequencies of the chromosomal types in the different canyons of the Panamint range are not alike, the fly population is certainly not panmictic. Whether or not migration of flies from canyon to canyon occurs, in any case the migration rate is not sufficient to prevent the origin of differences between the local colonies. In fact, our data suggest the existence of geographical gradients for some of the gene arrangements (fig. 2).

The frequency of Arrowhead seems to be highest in the southern part of the Panamints, and to decrease northward. Standard shows the opposite regularity. Tree Line is most frequent in the central portion of the range. In general, adjacent canyons are more similar than remote ones. This may be the result of occasional migration between the canyons. It is noteworthy that no geographical gradients are observed between *D. pseudoobscura* populations inhabiting separate mountain ranges; the migration of flies from range to range is certainly less probable than migration from canyon to canyon (DOBZHANSKY and QUEAL 1938).

The other important observation concerns the significant differences between the frequencies of the various gene arrangements on two successive years in the same canyon. This has been observed in the Wildrose canyon of the Panamint and in the San Gabriel canyon further south. On the other hand, populations of race A and race B remained stationary during the same period in Mount Whitney Canyon in the Sierra Nevada. It follows that yearly fluctuations in the genetical structure of a population may or may not occur. Such fluctuations can be accounted for on the same basis as the differentiation of the local populations in general. They may be due to a small effective size of the population in a breeding unit. It is very probable that the fly populations in the Death Valley region undergo sharp seasonal reductions and increases; the number of flies is reduced in winter due to cold, and perhaps also at the height of the summer due to extreme aridity. The reduction of population is normally proportional, that is, it affects all the genetical constituents to the same degree. But occasionally it may lead to a disproportionate change in the genetical structure. During the expansion of a population the relative frequencies of the genes or chromosome structures attained at the time of the greatest reduction are, more or less, faithfully perpetuated. On such a basis the genetic structure of a population in a locality may remain stationary over a period of years, or it may fluctuate; the fluctuation is, in general, greater when the minimum effective breeding size is smaller.

Whether or not the various gene arrangements in the third chromosome differ in adaptive value (due to position effects) is unknown. It is most probable that they are neutral in this respect. The whole complex of facts at hand can consistently be accounted for on the assumption of random variations in the frequencies of the gene arrangements and without the intervention of selection. The agreement of the observed and expected frequencies of the inversion homo- and heterozygotes shows that (1) random mating prevails, and (2) that the viabilities of the homo- and heterozygotes are alike. The occurrence of inversions or other structural changes in a chromosome does not *per se* lead to isolation or formation of endogamous groups within a population.

ACKNOWLEDGMENTS

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SUMMARY

1. The frequencies of the gene arrangements in the third chromosome of *Drosophila pseudoobscura* were determined in populations inhabiting the different canyons of the Panamint Mountains.

2. Six different gene arrangements are present in the populations, and their relative frequencies vary from canyon to canyon.

3. Populations of adjacent canyons are somewhat more similar than those of the more remote ones. The geographical gradient may be due to migration, which, however, is not effective enough to level the differences between the canyons.

4. The observed and expected frequencies of the inversion homozygotes and heterozygotes in the canyon populations are in agreement, indicating random mating and equal viability.

5. Significant yearly variations were found in the populations of two localities, but were not observed in a third.

6. The genetic differences between the canyon colonies, as well as the yearly variations in the frequencies of the gene arrangements, are probably due to the smallness of the effective breeding size of these colonies.

7. Local genetic diversification can arise in a population occupying a continuously habitable territory. How small the elementary breeding units are in such a territory remains to be determined.

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DISTINGUISHING BETWEEN TWO TYPES OF GENE ACTION IN QUANTITATIVE INHERITANCE

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INTRODUCTION

AMONG the widely divergent results obtained from "quantitative character" crosses one common type is characterized by (a) F_1 mean approaching that of the smaller parent strain and (b) positive skewness in the frequency distribution of F_2 measurements. Among many examples might be cited crosses involving differences of corolla tube length in tobacco (EAST 1913; SMITH 1937), fruit size in squash (SINNOTT 1937) in peppers (DALE 1929; KAISER 1935) and in tomatoes (MCARTHUR and BUTLER 1938), weight in chickens (JULL and QUINN 1931).

Results of this kind have long been recognized as incompatible with the early hypothesis that quantitative characters might be determined in general by genes having *arithmetic* effects without dominance or interaction. This hypothesis had been proposed (EAST 1910) as a reasonably simple scheme which might and did accord with the main features of size segregation in certain crosses. But other crosses, giving the sort of result under discussion here, were shown by EAST (1913) to be better accounted for if the relevant genes were assumed to have a multiplicative, or *geometric*, action. Many subsequent workers have adopted the same interpretation for comparable cases (DALE, SINNOTT and SMITH, among others).

LINDSTROM (1935) has proposed a partial return to the original hypothesis, in dealing with skewed distributions of fruit size in the progeny of hybrids between a small-fruited wild tomato and two large-fruited domesticated varieties, namely: that the factors have *arithmetic* effects, without interaction, but with *partial dominance* of the small size genes. In discussing his results LINDSTROM pointed out that " . . . it does not help matters by assuming dominance as a necessity in explaining the numerous facts of heterosis and prepotency, and then conveniently discarding dominance for most other forms of quantitative inheritance" and that " . . . the mere fact that quantitative character data seem to fit a logarithmic curve does not necessarily rule out dominance."

Perhaps neither scheme of gene effects will turn out ultimately to be strictly applicable. It seems likely, on the whole, that the genes determin-

[1] The senior author's part of the present study was done mostly during tenure of a National Research Council Fellowship in zoology at the University of Chicago (1935–36).

[2] The data presented under the junior author's name were obtained while at the Bussey Institution of Harvard University.

ing any particular size difference would be found, if isolated singly, to be rather diverse in nature of action and in synergetic relations as well as in magnitude of effect and degree of dominance. But the isolation of monogenic differences is generally so difficult in the case of quantitative characters that it is often practicable only to determine which of the commonly proposed simple schemes of inheritance comes nearest to compatibility with the data. For this purpose it would be desirable, as LINDSTROM's comments suggest, to examine the data in as many ways as possible.

A number of tests are available for determining whether the geometric or the arithmetic gene effect hypothesis is more nearly in accord with a particular set of data. To compile these tests and to add several new ones with a uniform system of proof, is the purpose of the following pages.

THE GENOTYPE-PHENOTYPE RELATION

The general features of the arithmetic scheme (with dominance) and of the geometric hypothesis are shown in table 1 which will be recognized

TABLE 1

Two sorts of genotype-phenotype relation in quantitative inheritance.

GENOTYPE	AVERAGE MEASUREMENT	
	ARITHMETIC EFFECTS SMALL DOMINANT	GEOMETRIC EFFECTS
1. $a_1a_1a_2a_2\cdots a_na_n$	A_0	A_0
2. $a_1'a_1a_2a_2\cdots a_na_n$	$A_0+\alpha_1-\delta_1$	$A_0(1+k_1)$
3. $a_1'a_1'a_2a_2\cdots a_na_n$	$A_0+2\alpha_1$	$A_0(1+k_1)^2$
4. $a_1a_1a_2'a_2\cdots a_na_n$	$A_0+\alpha_2-\delta_2$	$A_0(1+k_2)$
5. $a_1'a_1a_2'a_2\cdots a_na_n$	$A_0+\alpha_1-\delta_1+\alpha_2-\delta_2$	$A_0(1+k_1)(1+k_2)$
6. $a_1'a_1'a_2'a_2\cdots a_na_n$	$A_0+2\alpha_1+\alpha_2-\delta_2$	$A_0(1+k_1)^2(1+k_2)$
7. $a_1a_1a_2'a_2'\cdots a_na_n$	$A_0+2\alpha_2$	$A_0(1+k_2)^2$
8. $a_1'a_1a_2'a_2'\cdots a_na_n$	$A_0+\alpha_1-\delta_1+2\alpha_2$	$A_0(1+k_1)(1+k_2)^2$
9. $a_1'a_1'a_2'a_2'\cdots a_na_n$	$A_0+2\alpha_1+2\alpha_2$	$A_0(1+k_1)^2(1+k_2)^2$
m. $a_1'a_1'a_2'a_2'\cdots a_n'a_n'$	$A_0+2\alpha_1+2\alpha_2+\cdots+2\alpha_n$	$A_0(1+k_1)^2(1+k_2)^2\cdots(1+k_n)^2$

as merely an algebraic statement of the ideas proposed by EAST, with dominance added as a modification in the former case. The essential point of the arithmetic scheme is that a particular gene substitution always *adds* the same amount to the phenotypic value, whatever the remaining genotype. Dominance of small size is shown by representing the difference between $a_i'a_i$ and a_ia_i, $(\alpha_i-\delta_i)$, as less than the difference between $a_i'a_i'$ and $a_i'a_i$, $(\alpha_i+\delta_i)$. Here α_i represents one-half of the difference between $a_i'a_i'$ and a_ia_i; δ_i then represents the deviation of $a_i'a_i$ from true intermediacy. The essential point in the geometric case is that a given gene substitution is assumed always to *multiply* the phenotypic value by the same amount

(that is, to make the same percent increment), whatever the residual genotype. Since no "genic" dominance is ordinarily assumed in the geometric scheme $a_i'a_i'$ is as many times larger than $a_i'a_i$ as $a_i'a_i$ is than a_ia_i, namely by a factor which is here represented as $(1+k_i)$. Of course, as is readily seen, this relation leads to an apparent, "phenotypic," dominance.

The two sorts of gene action will generally yield unlike series of phenotypic values, although they both produce positively-skewed F_2's. For example, where $a_1a_1a_2a_2$ has the value 1 and $a_1'a_1'a_2'a_2'$ the value 16, intermediate genotypes will have values as shown in table 1A, if the two loci are of equal effect. In the arithmetic series the phenotypic effect of three different degrees of small-size dominance is represented.

TABLE 1A

Series of phenotypic values for different gene actions.

	GENOTYPE	a_1a_1 a_2a_2	$a_1'a_1$ a_2a_2	$a_1'a_1'$ a_2a_2	a_1a_1 $a_2'a_2$	$a_1'a_1$ $a_2'a_2$	$a_1'a_1'$ $a_2'a_2$	a_1a_1 $a_2'a_2'$	$a_1'a_1$ $a_2'a_2'$	$a_1'a_1'$ $a_2'a_2'$
PHENOTYPE	geometric effects $k=1$	1	2	4	2	4	8	4	8	16
	arithmetic effects									
	$\alpha=3.75$; $\delta=3.75$	1	1	8.5	1	1	8.5	8.5	8.5	16
	3.75 2.75	1	2	8.5	2	3	9.5	8.5	9.5	16
	3.75 2.25	1	2.5	8.5	2.5	4	10	8.5	10	16

TESTS INVOLVING AVERAGES

Arithmetic effects with dominance

Suppose that the size difference between two strains is determined by a number of non-linked genes with partial dominance of small size; furthermore, that each parent strain is isogenic, one carrying all the recessive alleles $a_1a_1a_2a_2\cdots a_na_n$, the other all the dominants $a_1'a_1'a_2a_2'\cdots a_n'a_n'$. The F_1, then, will be $a_1'a_1a_2'a_2\cdots a_n'a_n$. Suppose that the basic size (A_0) and the magnitudes of the gene effects (α's, δ's) were known as, for example, by a previous *very* large experiment in which individual gene differences had been isolated. Then the average size of the small strain individuals used as the start of a breeding experiment should be equal, within the limits of sampling error to A_0; the average size of the large strain parents, to $A_0+2\alpha_1+2\alpha_2+\cdots+2\alpha_n$, which may be represented by $A_0+2\Sigma\alpha$; the average size of the F_1 progeny, to $A_0+\Sigma\alpha-\Sigma\delta$.

Two sorts of quantities have to be clearly distinguished here:

(1) Statistical constants calculated by the usual methods from the measurements of groups of individuals used or obtained in quantitative character crosses. Examples of such quantities are $\bar{v}_0$, $\bar{v}_{0'}$, $\bar{v}_1$, $\bar{v}_2$, $\bar{v}_r$ and $\bar{v}_R$, the ob-

served average measurements of small and large parent strains, of F_1, F_2 and backcrosses to small and large parent strains, respectively.

(2) Expressions like $A_0+\Sigma\alpha-\Sigma\delta$ which represent *ideal* values of statistical constants (in this case, of $\bar{v}_1$) in terms of the size of individual factor effects. If these latter were known, the ideal and observed values should be found to be equal within the limits of sampling error. Since the gene effects cannot in general be evaluated they will be used here merely to establish what relations should be found among the observed statistical constants; they will not appear in the final criteria for compatibility of breeding data with the hypothesis of arithmetic (or geometric) effects.

In the light of the distinction just made it may be written that $\bar{v}_0 \doteq A_0$; $\bar{v}_{0'} \doteq A_0+2\Sigma\alpha$; $\bar{v}_1 = A_0+\Sigma\alpha-\Sigma\delta$. Here "$\doteq$" has the sense of "is an estimate of" or "should be equal to, within the limits of sampling error." Similarly, as will be shown in the following paragraph, $\bar{v}_2 \doteq A_0+\Sigma\alpha-\frac{1}{2}\Sigma\delta$. But from the previous expressions $[\bar{v}_0+2\bar{v}_1+\bar{v}_{0'}]/4 \doteq A_0+\Sigma\alpha-\frac{1}{2}\Sigma\delta$. Then since two observable quantities each estimate the same unknown, they should be equal within the limits of sampling error, if the genes involved actually have arithmetic effects. That is

$$\bar{v}_2 \doteq [\bar{v}_0 + 2\bar{v}_1 + \bar{v}_{0'}]/4. \qquad (1)$$

That $\bar{v}_2 \doteq A_0+\Sigma\alpha-\frac{1}{2}\Sigma\delta$ can be readily seen as follows. The ideal F_2 average could be obtained by making a table of expected frequencies and values of all F_2 genotypes and calculating $\bar{v}$ in the usual way. But since the phenotypic values (table 1, column 2) are the sums of values due to individual loci, the ideal F_2 average can also be calculated by the familiar method of adding the contributions from individual loci:

$$\begin{aligned}\bar{v}_2 &\doteq A_0 + [\tfrac{1}{4}(0) + \tfrac{1}{2}(\alpha_1 - \delta_1) + \tfrac{1}{4}(2\alpha_1)] + [\tfrac{1}{4}(0) + \tfrac{1}{2}(\alpha_2 - \delta_2) + \tfrac{1}{4}(2\alpha_2)] \\ &\quad + \cdots + [\tfrac{1}{4}(0) + \tfrac{1}{2}(\alpha_n - \delta_n) + \tfrac{1}{4}(2\alpha_n)] \\ &\doteq A_0 + (\alpha_1 + \alpha_2 + \cdots + \alpha_n) - \tfrac{1}{2}(\delta_1 + \delta_2 + \cdots + \delta_n) = A_0 + \Sigma\alpha - \tfrac{1}{2}\Sigma\delta.\end{aligned}$$

Criterion 1, which has been used by WRIGHT (1922), is applied to a part of LINDSTROM'S (1935) data in table 2. In each cross the F_2 mean is considerably smaller than would be expected if the gene effects were really arithmetic.

Criteria like (1) can also be found for the two backcrosses. For that to the small parent strain the ideal value of the average is

$$\begin{aligned}&A_0 + [\tfrac{1}{2}(0) + \tfrac{1}{2}(\alpha_1 - \delta_1)] + [\tfrac{1}{2}(0) + \tfrac{1}{2}(\alpha_2 - \delta_2)] + \cdots \\ &\quad + [\tfrac{1}{2}(0) + \tfrac{1}{2}(\alpha_n - \delta_n)] = A_0 + \tfrac{1}{2}\Sigma\alpha - \tfrac{1}{2}\Sigma\delta.\end{aligned}$$

That is, $\bar{v}_r \doteq A_0+\frac{1}{2}\Sigma\alpha-\frac{1}{2}\Sigma\delta$. But also $\frac{1}{2}(\bar{v}_0+\bar{v}_1) \doteq A_0+\frac{1}{2}\Sigma\alpha-\frac{1}{2}\Sigma\delta$. Hence

$$\bar{v}_r \doteq \tfrac{1}{2}(\bar{v}_0 + \bar{v}_1). \qquad (2)$$

In the backcross to the large parent strain the ideal value of the mean is $A_0+[\frac{1}{2}(\alpha_1-\delta_1)+\frac{1}{2}(2\alpha_1)]+[\frac{1}{2}(\alpha_2-\delta_2)+\frac{1}{2}(2\alpha_2)]+\cdots+[\frac{1}{2}(\alpha_n-\delta_n)+\frac{1}{2}(2\alpha_n)]$. That is $\bar{v}_R \doteq \frac{3}{2}\Sigma\alpha-\frac{1}{2}\Sigma\delta$. But also $\frac{1}{2}(\bar{v}_1+\bar{v}_{0'}) \doteq \frac{3}{2}\Sigma\alpha-\frac{1}{2}\Sigma\delta$. Hence

$$\bar{v}_R \doteq \tfrac{1}{2}(\bar{v}_1+\bar{v}_{0'}). \tag{3}$$

TABLE 2

Test of arithmetic nature of factor effects controlling fruit size in two tomato species crosses (data of LINDSTROM *1935).*

$\bar{v}_0$ (Red Currant)	1.0 gram	$\bar{v}_0$ (Red Currant)	1.0 gram
$\bar{v}_{0'}$ (Dwarf Oval)	22	$\bar{v}_{0'}$ (Dwarf Peach)	60.9
$\bar{v}_1$	4.58±0.18	$\bar{v}_1$	6.9
$\bar{v}_2$	4.63±0.15	$\bar{v}_2$	6.86±0.23
$(\bar{v}_0+2\bar{v}_1+\bar{v}_{0'})/4$	8.04	$(\bar{v}_0+2\bar{v}_1+\bar{v}_{0'})/4$	18.9

Relations (1), (2) and (3) should be found to hold in any cross where the relevant genes are non-linked and have arithmetic effects with partial dominance of small size even, it can be shown, if the small strain is homozygous for some large size genes, the large strain for the small size alleles.

Geometric effects

If the size difference between the two strains were determined by genes with geometric action and the genotypes were as in the previous section, then the ideal average measurements of the small parent, large parent and F_1 (table 1, column 3) would be A_0, $A_0(1+k_1)^2(1+k_2)^2\cdots(1+k_n)^2$ and $A_0(1+k_1)(1+k_2)\cdots(1+k_n)$. Hence the observable quantities $\bar{v}_1$ and $\sqrt{\bar{v}_0\cdot\bar{v}_{0'}}$ each estimate the same unknown and so

$$\bar{v}_1 \doteq \sqrt{\bar{v}_0\cdot\bar{v}_{0'}}. \tag{4}$$

The F_1 average should be the geometric mean of the parent averages, within the limits of sampling error, if the genes involved have geometric effects. This criterion has been used by LINDSTROM (1935) and by MACARTHUR and BUTLER (1938).

We proceed to calculate the ideal F_2 average. If the difference between parent strains were determined by only two loci there would be nine genotypic classes whose values in terms of gene effects are shown in table 1. The average can be obtained then by multiplying each ideal class value by its ideal frequency:

$$\begin{aligned}&\tfrac{1}{16}A_0+\tfrac{1}{8}A_0(1+k_1)+\tfrac{1}{16}A_0(1+k_1)^2+\tfrac{1}{8}A_0(1+k_2)+\tfrac{1}{4}A_0(1+k_1)(1+k_2)\\&\quad+\tfrac{1}{8}A_0(1+k_1)^2(1+k_2)+\tfrac{1}{16}A_0(1+k_2)^2+\tfrac{1}{8}A_0(1+k_1)(1+k_2)^2\\&\quad+\tfrac{1}{16}A_0(1+k_1)^2(1+k_2)^2=A_0(1+\tfrac{1}{2}k_1)^2(1+\tfrac{1}{2}k_2)^2.\end{aligned}$$

And it can be similarly shown that if n loci are involved

$$\bar{v}_2 \doteq A_0(1 + \tfrac{1}{2}k_1)^2(1 + \tfrac{1}{2}k_2)^2 \cdots (1 + \tfrac{1}{2}k_n)^2. \qquad (5)$$

This equation does not yield an expression analogous to (1) for a relation to be expected among parent, F_1 and F_2 observed averages. But if it is assumed that all of the genes (n in number) have approximately equal effects, an approach to the following relation is to be expected, especially where many gene differences are involved and the parent strains differ considerably in size:

$$\bar{v}_2 = \bar{v}_1\left[1 + \frac{1}{3n}(\log \bar{v}_{0'} - \log \bar{v}_0)^2\right]. \qquad (6)$$

That is, the F_2 average should in many cases be about equal to the F_1 as is ordinarily assumed (for example, MACARTHUR and BUTLER 1938, p. 255), but it need not always be so.

Criteria (4) and (6) are applied to LINDSTROM's data in table 3. The agreement between observed and expected values, although not totally satisfactory, is still somewhat better than that of table 2.

TABLE 3

Test of geometric nature of gene effects controlling fruit size in two tomato species crosses (data of LINDSTROM *1935).*

$\bar{v}_0$	1.0 gram	$\bar{v}_0$	1.0 gram
$\bar{v}_{0'}$	22	$\bar{v}_{0'}$	60.9
$\bar{v}_1$	4.58±0.18	$\bar{v}_1$	6.9
$\sqrt{\bar{v}_0 \cdot \bar{v}_{0'}}$ (from Lindstrom)	4.69	$\sqrt{\bar{v}_0 \cdot \bar{v}_{0'}}$ (from Lindstrom)	7.8
$\bar{v}_2$	4.63±0.15	$\bar{v}_2$	6.87±0.23
$\bar{v}_1 + \frac{\bar{v}_1}{3n}\left(\log\frac{\bar{v}_{0'}}{\bar{v}_0}\right)^2$	$n=5$ 5.1 $n=10$ 4.8	$\bar{v}_1 + \frac{\bar{v}_1}{3n}\left(\log\frac{\bar{v}_{0'}}{\bar{v}_0}\right)^2$	$n=5$ 8.4 $n=10$ 7.6

Relations like (4) can be found for the two backcrosses. The ideal average of the backcross to the small strain, where two genes are involved, is $\frac{1}{4}A_0 + \frac{1}{4}A_0(1+k_1) + \frac{1}{4}A_0(1+k_2) + \frac{1}{4}A_0(1+k_1)(1+k_2) = A_0(1+\frac{1}{2}k_1)(1+\frac{1}{2}k_2)$; or by analogy, where n loci are involved, $A_0(1+\frac{1}{2}k_1)(1+\frac{1}{2}k_2)\cdots(1+\frac{1}{2}k_n)$. This latter product may be represented by the symbol $A_0\Pi(1+\frac{1}{2}k_i)$. Hence

$$\bar{v}_r \doteq A_0\Pi(1 + \tfrac{1}{2}k_i). \qquad (7)$$

But the same unknown quantity is also estimated by the geometric mean of the F_2 and small parent averages: $\sqrt{\bar{v}_0 \cdot \bar{v}_2} \doteq A_0 \cdot \Pi(1+\frac{1}{2}k_i)$. So

$$\bar{v}_r \doteq \sqrt{\bar{v}_0 \cdot \bar{v}_2}. \qquad (8)$$

The ideal average of the backcross to the large strain is

$$\tfrac{1}{4}A_0(1 + k_1)(1 + k_2) + \tfrac{1}{4}A_0(1 + k_1)^2(1 + k_2) + \tfrac{1}{4}A_0(1 + k_1)(1 + k_2)^2 + \tfrac{1}{4}A_0(1 + k_1)^2(1 + k_2)^2;$$

or by analogy, where n loci are involved,

$$A_0(1 + k_1)(1 + k_2) \cdots (1 + k_n)(1 + \tfrac{1}{2}k_1)(1 + \tfrac{1}{2}k_2) \cdots (1 + \tfrac{1}{2}k_n).$$

That is

$$\bar{v}_R \doteq A_0\Pi(1 + k_i)\cdot\Pi(1 + \tfrac{1}{2}k_i). \tag{9}$$

But the same unknown is estimated by the geometric mean of the large parent and F_2 averages: $\sqrt{\bar{v}_0\cdot\bar{v}_2} \doteq A_0\Pi(1+k_i)\cdot\Pi(1+\frac{1}{2}k_i)$. Hence

$$\bar{v}_R \doteq \sqrt{\bar{v}_0\cdot\bar{v}_2}. \tag{10}$$

The criteria so far considered may be summarized as follows:

	geometric gene action is indicated if:	arithmetic gene action is indicated if:
F_1 average is:	geometric mean of parent averages	
F_2 average is:	not much larger than F_1	midway between F_1 and midvalue of parent averages
small backcross average is:	geometric mean of F_2 and small parent averages	midway between F_1 and small parent averages
large backcross average is:	geometric mean of F_2 and large parent averages	midway between F_1 and large parent averages.

All of these relations are to be expected, it can be shown, even where the small strain is homozygous for some of the large size genes, the large strain for the small size alleles, so long as the loci are not linked.

It may be recalled here that averages have sometimes been used differently in applying the hypothesis of geometric gene effects, for example by WRIGHT (1922), DALE (1929), and SMITH (1937). The observed measurements have been converted into logarithms, whose averages and variances have then been tested for the numerical relations characteristic of arithmetic gene action. Aside from the nature of the non-genetic variation this procedure should be correct since a factor which multiplies the phenotype has an additive effect on the logarithm. But it can readily be seen that the method is strictly applicable only where the frequency distributions of the logarithms of parent and F_1 measurements are more nearly normal than the distributions of the untransformed measurements. The present treatment assumes that it is ordinarily the measurements, rather than their logarithms, which are normally distributed.

TESTS INVOLVING STANDARD DEVIATIONS

The problem here is analogous to that of the previous section: to find "$\doteq$" relations connecting the observable standard deviations with the un-

known gene effects, and through these relations to find others involving only the observable constants.

For subsequent use there may be recalled here some of the statistical properties of segregating generations in quantitative character crosses. (1) In most cases there is considerable non-genetic variability; that is, individuals of the same genotype have rather diverse measurements which often coincide with the measurements of individuals of other genotypes. If the component genotypic groups of a segregating generation could be separated, one could calculate the average and non-genetic variance, v_c and σ_c^2 of each genotype. (2) There is also genetic variability; that is, different genotypes have different average measurements. (3) If genotypes could be separated the variance of a segregating generation as a whole could be calculated by either of two well-known methods giving identical results:

(a) $\sigma^2 = \frac{1}{N}\Sigma(v_i - \bar{v})^2$. This is of course the customary method which would be used in calculating the variance of any actual data. In this form there are as many classes as individual measurements; v_i represents an individual measurement and $\bar{v}$, the mean of the whole generation.

(b) $\sigma^2 = \Sigma f_c(v_c - \bar{v})^2 + \Sigma f_c\sigma_c^2$. Here there are only as many classes as genotypes; f_c is the proportional frequency of a genotype. It will be noticed that the first term involves only the class averages and the mean of the whole generation and so is independent of the extent of non-genetic variability. It is the "genetic" portion of the variance. The second term involves only the non-genetic variance of measurements within the several genetic classes and so is independent of the differences in average measurement among genotypes. It is the "non-genetic" portion of the variance. (4) Even though genotypes cannot in most cases be separated, it is still possible to *estimate* how much of the variance of a segregating generation is genetic, and how much non-genetic. Presumably those three classes which have the same genotypes as the parents and F_1 will have the same non-genetic variances which may be represented by σ_0, $\sigma_{0'}$ and σ_1 respectively. Now rather commonly σ_0, $\sigma_{0'}$ and σ_1 fall approximately along a straight line when plotted against $\bar{v}_0$, $\bar{v}_{0'}$ and $\bar{v}_1$; and the non-genetic variability at any point along this line may be estimated by $\sigma_c = a + bv_c$, where a is the height of the line at the zero point of the v scale and b is the slope of the line. This relation might reasonably be supposed to hold for all genetypes in a segregating generation if it holds for the parental and F_1 types. Hence it is possible to estimate the total non-genetic variance:

$$\Sigma f_c\sigma_c^2 \doteq \Sigma f_c(a + bv_c)^2 = \Sigma f_c[(a + b\bar{v}) + b(v_c - \bar{v})]^2$$

$$\doteq (a + b\bar{v})^2 + b^2\Sigma f_c(v_c - \bar{v})^2.$$

Since the genetic variance is the difference between the total observed and the non-genetic variances, it follows that

$$\sigma^2 - (a + b\bar{v})^2 - b^2\Sigma f_c(v_c - \bar{v})^2 \doteq \Sigma f_c(v_c - \bar{v})^2$$

$$\frac{\sigma^2 - (a + b\bar{v})^2}{1 + b^2} \doteq \Sigma f_c(v_c - \bar{v})^2.$$

That is, the genetic portion of the variance of any segregating generation can be estimated by an operation which involves only the means and total variances of that generation and of the three non-segregating generations. The estimated *actual* genetic variances of the three segregating generations, obtained in this way, may be represented for brevity in subsequent reference by s_r^2, s_R^2 and s_2^2.

The next step, after determining how the genetic variance can be estimated from the actual data, is to find tests which will relate these corrected standard deviations to the gene effects, and which can be used as criteria for determining types of gene action.

The *ideal* variances of the segregating generations, in terms of gene effects, can be readily obtained. In the F_2, if, for example, only two loci are involved,

$$\begin{aligned}\Sigma f_c(v_c - \bar{v})^2 = \Sigma f_c v_c^2 - \bar{v}^2 = {} & \tfrac{1}{16}A_0^2 + \tfrac{1}{8}A_0^2(1 + k_1)^2 + \tfrac{1}{16}A_0^2(1 + k_1)^4 \\ & + \tfrac{1}{8}A_0^2(1 + k_2)^2 + \tfrac{1}{4}A_0^2(1 + k_1)^2(1 + k_2)^2 \\ & + \tfrac{1}{8}A_0^2(1 + k_1)^4(1 + k_2)^2 + \tfrac{1}{16}A_0^2(1 + k_2)^4 \\ & + \tfrac{1}{8}A_0^2(1 + k_1)^2(1 + k_2)^4 + \tfrac{1}{16}A_0^2(1 + k_1)^4(1 + k_2)^4 \\ & - A_0^2(1 + \tfrac{1}{2}k_1)^4(1 + \tfrac{1}{2}k_2)^4 \\ = {} & A_0^2(1 + k_1 + \tfrac{1}{2}k_1^2)^2(1 + k_2 + \tfrac{1}{2}k_2^2)^2 - A_0^2(1 + \tfrac{1}{2}k_1)^4(1 + \tfrac{1}{2}k_2)^4.\end{aligned}$$

This ideal quantity, if it could be determined, should be equal within the limits of sampling error to the corresponding genetic variance s_2^2 estimated from the actual data. That is, for n loci, $s_2^2 \doteq A_0^2 \cdot \Pi(1+k+\frac{1}{2}k^2)^2 - A_0^2 \cdot \Pi(1+k)^4$. Or from (5) above

$$s_2^2 + \bar{v}_2^2 \doteq A_0^2 \cdot \Pi(1 + k + \tfrac{1}{2}k^2)^2. \tag{11}$$

In the backcross to the small parent strain, where two loci are involved

$$\begin{aligned}\Sigma f_c(v_c - \bar{v})^2 = {} & \tfrac{1}{4}A_0^2 + \tfrac{1}{4}A_0^2(1 + k_1)^2 + \tfrac{1}{4}A_0^2(1 + k_2)^2 \\ & + \tfrac{1}{4}A_0^2(1 + k_1)^2(1 + k_2)^2 - A_0^2(1 + \tfrac{1}{2}k_1)^2(1 + \tfrac{1}{2}k_2)^2 \\ = {} & A_0^2(1 + k_1 + \tfrac{1}{2}k_1^2)(1 + k_2 + \tfrac{1}{2}k_2^2) - A_0^2(1 + \tfrac{1}{2}k_1)^2(1 + \tfrac{1}{2}k_2)^2.\end{aligned}$$

That is, for n loci, $s_r^2 \doteq A_0^2 \cdot \Pi(1+k+\frac{1}{2}k^2) - A_0^2 \cdot \Pi(1+\frac{1}{2}k)^2$. Or from (7) above

$$s_r^2 + \bar{v}_r^2 \doteq A_0^2 \cdot \Pi(1 + k + \tfrac{1}{2}k^2). \tag{12}$$

In the backcross to the large strain, where two loci are involved,

$$\Sigma f_c(v_c - \bar{v})^2 = \tfrac{1}{4}A_0^2(1 + k_1)^2(1 + k_2)^2 + \tfrac{1}{4}A_0^2(1 + k_1)^4(1 + k_2)^2 + \tfrac{1}{4}A_0^2(1 + k_1)^2(1 + k_2)^4 + \tfrac{1}{4}A_0^2(1 + k_1)^4(1 + k_2)^4 - A_0^2(1 + k_1)^2(1 + k_2)^2(1 + \tfrac{1}{2}k_1)^2(1 + \tfrac{1}{2}k_2)^2.$$

That is, where n loci are involved,

$$s_R^2 \doteq A_0^2 \cdot \Pi(1 + k)^2 \cdot \Pi(1 + k + \tfrac{1}{2}k^2) - A_0^2 \cdot \Pi(1 + k)^2 \cdot \Pi(1 + \tfrac{1}{2}k)^2.$$

And so from (9)

$$s_R^2 + \bar{v}_R^2 \doteq A_0^2 \cdot \Pi(1 + k)^2 \cdot \Pi(1 + k + \tfrac{1}{2}k^2). \tag{13}$$

Dividing (11), (12), (13) in order by the squares of (5), (7), (9) gives

$$\frac{s_2^2}{\bar{v}_2^2} + 1 \doteq \Pi(1 + k + \tfrac{1}{2}k^2)^2/\Pi(1 + \tfrac{1}{2}k)^4$$

$$\frac{s_r^2}{\bar{v}_r^2} + 1 \doteq \Pi(1 + k + \tfrac{1}{2}k^2)/\Pi(1 + \tfrac{1}{2}k)^2$$

$$\frac{s_R^2}{\bar{v}_R^2} + 1 \doteq \Pi(1 + k + \tfrac{1}{2}k^2)/\Pi(1 + \tfrac{1}{2}k)^2.$$

Hence,

$$s_r/\bar{v}_r \doteq s_R/\bar{v}_R \tag{14}$$

$$\left(1 + \frac{s_2^2}{\bar{v}_2^2}\right) \doteq \left(1 + \frac{s_r^2}{\bar{v}_r^2}\right)\left(1 + \frac{s_R^2}{\bar{v}_R^2}\right) \tag{15}$$

A simpler, approximate, form of (15) is

$$\frac{s_2}{\bar{v}_2} \doteq \frac{\sqrt{2}}{2}\left(\frac{s_r}{\bar{v}_r} + \frac{s_R}{\bar{v}_R}\right) \doteq \sqrt{2}\,\frac{s_r}{\bar{v}_r} \doteq \sqrt{2}\,\frac{s_R}{\bar{v}_R}. \tag{15a}$$

Thus in any cross where the genes involved have geometric effects the "coefficient of genetic variability," $s/\bar{v}$, should be found to have about the same value in both backcrosses and to be about 1.4 times as large in the F_2. No such simple criteria can be reached for arithmetic effects with dominance unless assumptions are made about the degree of dominance and the magnitudes of the individual gene effects.

TESTS INVOLVING SKEWNESS

As is well known third moments, like standard deviations, could be calculated in either of two ways if genotypic classes could be separated in the segregating generations:

(a) $\mu = \frac{1}{N}\Sigma(v_i - \bar{v})^3$ or

(b) if the non-genetic variation within classes is not skewed

$$\mu = \Sigma f_c(v_c - \bar{v})^3 + \Sigma f_c(v_c - \bar{v})\sigma_c^2.$$

(The symbols here have the same meaning as in the previous section.) Of the two terms on the right the first may be regarded as the "genetic" third moment since it depends only on the genetically determined differences in average measurement of genetic classes. The second term may be regarded as the "non-genetic" portion of the third moment since its value would be zero if there were no non-genetic variability (each $\sigma_c^2 = 0$).

Even where genotypic classes cannot be separated it is still possible to *estimate* the genetic third moment of a segregating generation. If $\sigma_c = a + bv_c$ at least approximately, it can be shown that

$$\Sigma f_c(v_c - \bar{v})\sigma_c^2 = 2b(a + b\bar{v})s^2 + b^2\Sigma f_c(v_c - \bar{v})^3.$$

(Here s^2 is the genetic variance estimated as seen in the previous section.) Hence, from (b)

$$\Sigma f_c(v_c - \bar{v})^3 = [\mu - 2b(a + b\bar{v})s^2]/(1 + b^2).$$

That is, the genetic third moment of any segregating generation can be estimated by an operation which involves the actual total third moment, total variance and mean of that generation and the means and variances of the three non-segregating generations. For brevity in subsequent reference the *actual* genetic third moments of the three segregating generations, so estimated, may be represented by m_2, m_r and m_R.

Since the genetic third moment depends only on class averages its *ideal* value can be expressed in terms of gene effects by substituting the proper class values from table 1, with the appropriate ideal frequencies, into the expression $\Sigma f_c(v_c - \bar{v})^3$. Using the class values for geometric effects leads to the relations

$$m_2/\bar{v}_2^3 + 3s_2^2/\bar{v}_2^2 + 1 \doteq \Pi(1 + k + k^2)^2/\Pi(1 + \tfrac{1}{2}k)^4$$

$$m_r/\bar{v}_r^3 + 3s_r^2/\bar{v}_r^2 + 1 \doteq \Pi(1 + k + k^2)/\Pi(1 + \tfrac{1}{2}k)^2$$

$$m_R/\bar{v}_R^3 + 3s_R^2/\bar{v}_R^2 + 1 \doteq \Pi(1 + k + k^2)/\Pi(1 + \tfrac{1}{2}k)^2.$$

Hence, since $s_r^2/\bar{v}_r^2 \doteq s_R^2/\bar{v}_R^2$,

$$m_r/\bar{v}_r^3 \doteq m_R/\bar{v}_R^3 \tag{16}$$

$$(m_2/\bar{v}_2^3 + 3s_2^2/\bar{v}_2^2 + 1) \doteq (m_r/\bar{v}_r^3 + 3s_r^2/\bar{v}_r^2 + 1)(m_R/\bar{v}_R^3 + 3s_R^2/\bar{v}_R^2 + 1) \tag{17}$$

An approximate form of (17) is

$$t_2 \doteq 0.63(t_r + t_R)\left[1 + \frac{(c_r + c_R)^4}{2(t_r + t_R)^3}\right]. \tag{17a}$$

Here t represents $\sqrt[3]{m}/\bar{v}$; c represents $s/\bar{v}$. Neither of these criteria could be significantly applied except to extensive data as the statistical constants involved, particularly the third moments, have large sampling errors.

TABLE 4

Tests of geometric vs. arithmetic gene effects in inheritance of corolla tube length in crosses between Nicotiana Langsdorffii and N. Sanderae.

A. *Data for estimating non-genetic variability corrections.*

	LANGS.—SMALL			F_1 (LANGS.×SAND.)			SAND.—LARGE			$\sigma = a + b\bar{v}$
	$\bar{v}_0$	σ_0	N_0	$\bar{v}_1$	σ_1	N_1	$\bar{v}_{0'}$	$\sigma_{0'}$	$N_{0'}$	
1933	19.1	0.72	32	36.5	2.08	51	70.8	4.54	25	$\sigma = -0.654 + 0.0736\bar{v}$
1934	18.9	0.60	28	38.5	2.53	8	69.3	4.08	47	$\sigma = -0.595 + 0.0680\bar{v}$
1935	19.1	0.57	19	38.2	1.63	8	71.8	4.74	14	$\sigma = -1.047 + 0.0795\bar{v}$
Total	19.1	0.64	79	36.9	2.09	67	70.1	4.33	86	$\sigma = -0.668 + 0.0717\bar{v}$

Using class values from table 1 we obtain for the relation among genetic third moments to be expected where factors have *arithmetic* effects:

$$m_r \doteq m_R \doteq 0. \tag{18}$$

HUTCHINSON (1936) has stated that with arithmetic gene effects "Skewness due to dominance is to be expected in F_2 only, a backcross giving a

TABLE 4B

Tests of averages.

	F_1				F_2			
	OBS.	EXPECTED		N	OBS.	EXPECTED		N
		GEOMETRIC $\sqrt{\bar{v}_0 \cdot \bar{v}_{0'}}$	ARITHMETIC			GEOMETRIC $\bar{v}_1+$	ARITHMETIC $(\bar{v}_0+2\bar{v}_1+\bar{v}_{0'})/4$	
1933	36.5	*36.8*	—	51	29.1	*36.5+*	*40.7*	139
1934	38.5	*36.2*	—	8	38.7	*38.5+*	*41.3*	238
1935	38.2	*37.0*	—	8	39.6	*38.2+*	*41.8*	177
Total	36.9	*36.6*	—	67	36.7	*36.9+*	*40.8*	554
	BACKCROSS TO SMALL				BACKCROSS TO LARGE			
	OBS.	EXPECTED			OBS.	EXPECTED		
		$\sqrt{\bar{v}_0 \cdot \bar{v}_2}$	$(\bar{v}_0+\bar{v}_1)/2$			$\sqrt{\bar{v}_2 \cdot \bar{v}_{0'}}$	$(\bar{v}_1+\bar{v}_{0'})/2$	
1933	23.8	*23.6*	*27.8*	279	44.9	*45.4*	*53.7*	108
1934	25.2	*27.0*	*28.7*	34	50.6	*51.8*	*53.9*	24
1935	27.2	*27.5*	*28.7*	74	53.6	*53.3*	*55.0*	74
Total	24.6	*26.5*	*28.0*	387	49.7	*50.7*	*53.5*	206

TABLE 4C

Tests of standard deviations.

	OBSERVED			CORRECTED $s=\sqrt{\sigma^2-(a+b\bar{v})^2}$			"COEFFICIENT OF GENETIC VARIABILITY" $c=s/\bar{v}$		
	σ_r	σ_R	σ_2	s_r	s_R	s_2	c_r	c_R	c_r
1933	2.38	3.99	3.08	2.10	2.95	2.67	0.087	0.065	0.090
1934	2.45	4.98	5.95	2.17	4.06	5.59	0.086	0.080	0.143
1935	3.47	6.95	6.34	3.35	6.15	5.98	0.137	0.114	0.150
Total	2.63	5.35	5.52	2.38	4.53	5.15	0.096	0.092	0.140
				Expected geometric:			*0.094*	*0.094*	*0.133*
							$=(c_r+c_R)/2$;		
							$=(c_r+c_R)/\sqrt{2}$		

symmetrical genetic distribution"; MACARTHUR and BUTLER (1938, p. 257) make a similar statement. But if $m=\mu-2b(a+b\bar{v})s^2\doteq 0$, $\mu\doteq 2b(a+b\bar{v})s^2$. That is, the observed total third moment is *not* expected to be zero except in the probably special case that all genotypic classes have about the same non-genetic variability. In this case $b=0$, and $\mu_r\doteq\mu_R\doteq 0$.

Whether the gene effects are arithmetic or geometric, the two backcrosses are expected to have about equal "coefficients of genetic third moment" $\sqrt[3]{m}/\bar{v}$. But the coefficients should be approximately zero in the former case, significantly different from zero in the latter.

USE OF CRITERIA FOR NATURE OF GENE EFFECTS

As an example of their use, the criteria for the two schemes of factor action are applied, in table 4, to data of SMITH (1937) on the inheritance of corolla tube length in crosses between *Nicotiana Langsdorffii* (small par-

TABLE 4D

Test of third moments (combined data).

	OBSERVED			CORRECTED $m=\mu-2b(a+b\bar{v})s^2$			"COFFFICIENT OF GENETIC THIRD MOMENT" $t=\sqrt[3]{m}/\bar{v}$		
μ_r	μ_R	μ_2	m_r	m_R	m_2	t_r	t_R	t_2
3.977	129.2	100.8	3.091	120.8	93.31	0.059	0.101	0.123
			expected arithmetic:			*0*	*0*	—
			expected geometric:			*0.080*	*0.080*	*0.116*
						$=(t_r+t_R)/2$;		
						$=0.63\,(t_r+t_R)\left[1+\frac{(c_r+c_R)^4}{2(t_r+t_R)^3}\right]$		

ent) and *N. Sanderae* (large parent). By each test the consequences of geometric gene effects give a reasonable approximation to the observed data; the values expected on arithmetic gene action deviate consistently. This is in agreement with SMITH'S (1937) conclusion from other analytical methods.

SUMMARY

Derivations have been given for a number of relations which should be found to hold, within the limits of sampling error, among the statistical constants of various generations in a quantitative character cross if the factors involved have arithmetic effects with partial dominance of small size. Other relations have been derived which should be found if the genes have geometric effects. These relations can be used as criteria of the nature of gene action in a quantitative cross, supplementing the methods already used, for example, by SINNOTT (1937) and LINDSTROM (1935).

The statistical constants involved are:

AVERAGES, VARIANCES AND THIRD MOMENTS:		DERIVED CONSTANTS:	
small strain:	$\bar{v}_0\ \sigma_0^2$	a, b:	constants relating standard deviation to average, in parent strains and F_1; $\sigma_0 = a + b\bar{v}_0$; $\sigma_1 = a + b\bar{v}_1$; $\sigma_{0'} = a + b\bar{v}_{0'}$.
large strain:	$\bar{v}_{0'}\ \sigma_{0'}^2$		
F_1:	$\bar{v}_1\ \sigma_1^2$		
F_2:	$\bar{v}_2\ \sigma_2^2\ \mu_2$	s^2:	estimate of portion of variance due to gene segregation, in a particular generation; $s^2 = [\sigma^2 - (a+b\bar{v})^2]/(1+b^2)$
BC to small	$\bar{v}_r\ \sigma_r^2\ \mu_r$		
BC to large:	$\bar{v}_R\ \sigma_R^2\ \mu_R$	c:	"coefficient of genetic variability"; $c = s/\bar{v}$
		m:	estimate of portion of third moment due to gene segregation, in a particular generation; $m = [\mu - 2b(a+b\bar{v})s^2]/(1+b^2)$
		t:	"coefficient of genetic third moment"; $t = \sqrt[3]{m}/\bar{v}$

The relations among these constants to be expected, within the limits of sampling error, for the two sorts of gene action are:

	ARITHMETIC EFFECTS SMALL PARTIALLY DOMINANT		GEOMETRIC EFFECTS
1.	$\bar{v}_2 = (\bar{v}_0 + 2\bar{v}_1 + \bar{v}_{0'})/4$	1.	$\bar{v}_1 = \sqrt{\bar{v}_0 \cdot \bar{v}_{0'}}$ (v_2 should generally be not much larger than v_1)
2.	$\bar{v}_r = (\bar{v}_0 + \bar{v}_1)\mu 2$	2.	$\bar{v}_r = \sqrt{\bar{v}_0 \cdot \bar{v}_2}$
3.	$\bar{v}_R = (\bar{v}_1 + \bar{v}_{0'})/2$	3.	$\bar{v}_R = \sqrt{\bar{v}_2 \cdot \bar{v}_{0'}}$
		4.	$c_r = c_R$
		5.	$c_2 = 0.71\ (c_r + c_R)$
4.	$t_r = t_R = 0$	6.	$t_r = t_R \neq 0$

The application of these tests to a group of suitable data on quantitative inheritance was demonstrated.

These relations are to be expected even (a) where the small strain is homozygous for some large size genes, the large strain for the small size alleles, and (b), in the case of arithmetic effects, where large size rather than small is dominant, or where there is no dominance, so long as the loci involved segregate independently or very nearly so.

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A DELAYED CHANGE OF PHENOTYPE FOLLOWING A CHANGE OF GENOTYPE IN PARAMECIUM AURELIA

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INTRODUCTION

THE present investigation, dealing with a delayed change of phenotype following a change of genotype, was performed on the stock S of the ciliate protozoan *Paramecium aurelia*. This stock is known (SONNEBORN 1937) to consist of two classes of individuals. When animals of one class are mixed with those of the other, they immediately form clumps and soon pair off for mating; but when animals of the same class are mixed, no such clumping and pairing occurs. As the conjugant pairs that form always consist of one animal of each class, the classes (originally called sexes I and II) have been designated mating types I and II (SONNEBORN 1938).

So long as nuclear reorganization does not occur, all the vegetative progeny of a single individual of either type are ordinarily of the same type as that individual; but after such a reorganization the mating types are redetermined in definite ratios. It thus happens that following nuclear reorganization some lines of descent are of the same mating type as before and some are now of different type. These relations are set forth in the papers of SONNEBORN (1937) and KIMBALL (1937). In the present paper, it will be shown that in the case of the change of genotype from type II before nuclear reorganization to type I afterwards, at least some animals remain phenotypically type II for a short time after the change. This is shown by the fact that at this time some of the animals give the mating reaction when mixed with type I. It will further be shown that the change of phenotype occurs at different rates in different individuals of the same culture, for at the same time that some react with type I others react with type II. Thus as both type I and type II animals are present in the same culture, conjugation can and does occur between them. In such cases, however, all the vegetative progeny are later exclusively of type I, even the descendants of those that were type II at an earlier stage. This shows that all animals were, from the first, genotypically type I even when they behaved, during a brief period, as type II. These phenomena are obviously of importance in relation to the problem of the interaction of the genes and the cytoplasm.

[1] The writer is deeply indebted to Dr. T. M. Sonneborn for the interest that he has taken in the work and for his many valuable suggestions concerning it.

In the present work, attention was confined to the changes occurring at the nuclear reorganization process, commonly known as endomixis, that occurs periodically within single unmated individuals. The essential features of this process for present purposes are the disintegration and eventual disappearance of the old macronucleus and the derivation of two new macronuclei from the micronuclei. Of these two macronuclei, one passes undivided to each of the daughter cells formed at the first fission. At subsequent fissions, the new macronuclei divide normally; and the fragments of the old macronucleus gradually disappear though they persist in diminishing numbers for several fissions. All the vegetative progeny of an individual containing only one new macronucleus are, ordinarily, genetically alike in mating type. Such a group of individuals is known as a "caryonide" (SONNEBORN 1938).

MATERIAL AND METHODS

To obtain material for the experiments, it was necessary to start out with caryonides of type II, induce endomixis in them, isolate the new caryonides, and ascertain which had changed genotypically to type I. This was done in the following way. Caryonide cultures were tested against standard cultures of the two mating types. Those that conjugated with type I but not with type II were of type II and suitable for further work. Endomixis was induced in such cultures according to the method of SONNEBORN (1937a); and individuals in endomixis were isolated. After the first fission of each isolated animal, one daughter cell was stained and the other kept alive. If the stained animal was in endomixis and contained not more than one new macronucleus, the living sister animal was retained as the progenitor of a caryonide; otherwise it was discarded. The new caryonides were all cultivated as daily isolation lines; that is, each day one animal was transferred from the previous day's culture to two drops of fresh culture medium in a fresh depression slide. The animals left over after the isolations of the first two or more days were kept without addition of culture medium for further study.

Not all these caryonides, however, were studied in detail; for, since many of them were type II and thus not suitable for study, this would have involved much unnecessary labor. Detailed studies were made only on those caryonides in which conjugants appeared in the first or second left-over cultures. The appearance of conjugants, suggesting the presence at this time of animals of both mating types in cultures presumably pure for one genotype, marked out these caryonides for the study of delayed changes of phenotype. Therefore, all other carynonides were discarded. Observations for conjugation were made on later left-over cultures of the caryonides retained in order to ascertain whether the occurrence of both

types was a transient or permanent characteristic. Tests for mating type were also made on one or more left-over cultures (but not the first one) in order to ascertain whether these caryonides were actually genotypically type I. All of the caryonides dealt with in this paper were genotypically type I. However, a few whose behavior was very different from the rest are to be reported upon elsewhere.

This method of selecting the material involved as an essential the detection of conjugation in the left-over cultures as quickly as possible. As decrease in the available food is necessary for conjugation to occur, the left-over cultures were made with as little of the nutrient culture fluid as practicable (2 drops). Observations for conjugation were made on these cultures at not greater than eight hour intervals from the time that 8 to 16 animals were present until the cultures were completely starved and there was no further likelihood of conjugation occurring. These observations were invariably made on the first two left-over cultures and frequently also on later ones.

It was essential, furthermore, to be sure that the conjugation which occurred was not the consequence of a new endomixis which would produce animals of both mating types. Therefore, samples of the isolation lines and left-over cultures were stained and examined frequently. In a few rare cases, endomixis was found in the first few days after the previous endomixis; but otherwise it was not found until 10 days after it. All caryonides in which very early endomixis was found were discarded.

THE EARLY PRESENCE OF BOTH MATING TYPES

Of the 141 available caryonides that had been changed by endomixis from type II to type I,[2] 21 were tested for the presence of both mating types in the first left-over culture. To do this it was desirable to pick out for testing animals of each mating type if such existed in these cultures. Therefore advantage was taken of the occurrence of conjugation; for presumably when two individuals come together for conjugation, they are of different mating types. This matter was put to a direct test by isolating pairs that had just come together for mating but were not yet firmly united. These were then separated by drawing them in and out of a pipette a few times, and the two animals thus separated (called hereafter a "split pair") were individually tested for mating type. The tests were carried out

[2] This total of 141 caryonides includes the 17 found in one experiment in which there appears to have been an error in labelling. These 17, according to the records, came from a single culture, marked type I, in which endomixis had been induced. In the same petri dish was another culture marked type II. The caryonides isolated from these two cultures showed by their subsequent behavior just the reverse of what would have been expected from the labels. Hence, it is assumed that the labels were inadvertently reversed and that the 17 caryonides in question actually came from a culture which, before endomixis, was type II instead of type I.

as shown in figure 1. Each member of a split pair was placed separately with a group of animals of known mating type, in some cases type I and in some cases type II; and observations for mating reactions were made. The animals of known mating type were always considerably larger in size than the animals to be tested so that in all cases it was possible to identify the latter. In every case in this first part of the test, only one member of the split pair gave the mating reaction. After about one-half to

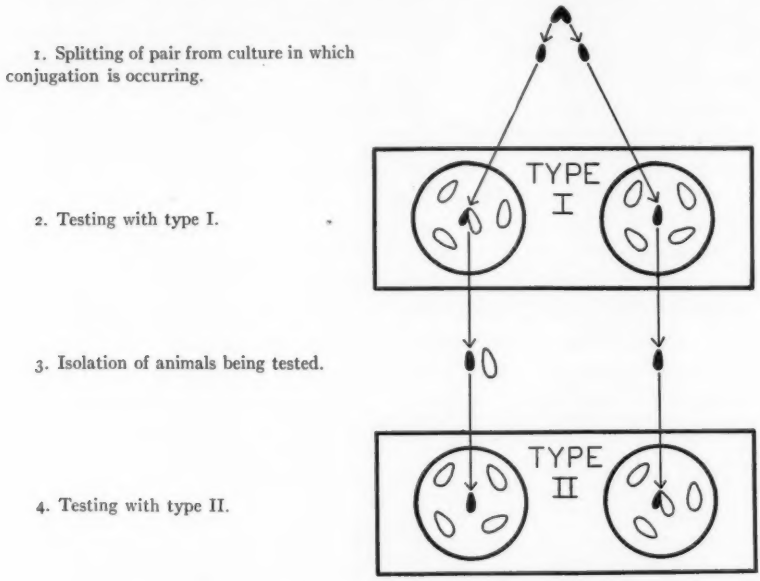
1. Splitting of pair from culture in which conjugation is occurring.
2. Testing with type I.
3. Isolation of animals being tested.
4. Testing with type II.
TYPE I
TYPE II

FIGURE 1.—Diagram showing the method used to test the two members of a split pair individually for mating type. The animals shown in solid black are those being tested for mating type. Those shown in outline are the animals of known mating type used for the testing.

three-quarters of an hour, the members of the original split pair as identified by their smaller size were withdrawn and placed with large animals of the other mating type. Again not more than one member of the original split pair reacted and this time it was the one that had not reacted in the first part of the test. Thus one member of the original split pair reacted with type I but not with type II; and the other member with type II but not type I. Hence, one member of the original pair was of type I and the other of type II.

The complete demonstration that conjugation in these cultures occurred between type I and type II animals was made for 16 of the 22 pairs tested.

In the other 6 pairs, only one member of each pair reacted. This one, however, reacted with type I alone; and so it was type II. Nevertheless, as will be shown later, this animal as well as the other one gave rise, when they were allowed to multiply, to type I animals only. Several other pairs, not recorded here since they yield no information on the question in hand, either entirely failed to react; or, if one member of the pair did react, it did so as type I. Why some of the animals did not react is not certain.

The foregoing analysis showed not only that the 21 caryonides whose split pairs were tested contained both types I and II but also that the occurrence of conjugation within a culture is evidence that both types are present, for conjugation has been shown to occur only between these two types. Hence, the remaining 120 caryonides for which no split pairs were individually tested must have contained animals of both types for conjugation occurred in them also.

THE PRESENCE OF BOTH TYPES A TRANSIENT PHENOMENON

Further study demonstrates that the presence of both types in these caryonides is a transient phenomenon; for conjugation, which is evidence for the presence of both types, occurred only in the early left-over cultures of these caryonides. Conjugants were found only in the first left-over culture in the case of 124 caryonides, including the 21 whose split pairs were tested individually for mating type. They were found in the first two left-over cultures but in no later ones in the case of 13 caryonides and in only the second left-over culture in the case of 4 caryonides. No pairs were found in any later cultures. In this study, two successive cultures were examined for 32 caryonides, three for 99, and four for 10.

GENETIC MATING TYPE OF THE CARYONIDES

It is clear from the evidence that even the type II animals of the first left-over cultures must have been genetically type I. In every case, at least one left-over culture, but not the first, was tested for mating type. Every one of the 141 caryonides dealt with here reacted in these tests solely as type I. Thirteen caryonides, not otherwise included in the discussion, though they reacted for the most part as type I did give a weak reaction as type II in at least one test. Eight of these were found in one experiment in which there was cause to suspect that the standard cultures used for the first two tests were not pure for one mating type. A fourth left-over culture of 6 of these 8 caryonides was tested with fresh standard cultures which were certainly pure for one mating type; and, in every case, this last culture reacted solely as type I. It is not impossible that the standard cultures used to test the other five caryonides were likewise impure. It seems probable, then, that the reason some of the left-over cultures of each

of these thirteen caryonides reacted with both standard cultures was that the standard cultures themselves contained animals of both types.

More direct evidence that all animals of the 141 caryonides with which this paper for the most part deals were genotypically type I is furnished by a study of cultures derived from the members of split pairs. Animals which had recently come together for conjugation were split and each animal isolated separately. In the case of the 22 pairs whose members were tested individually for mating type, the animals were isolated after the testing had been completed. In all cases, these isolated animals were allowed to divide once; and one of the two sister animals was stained and examined for signs of nuclear reorganization. In the cases considered here, none was found; and the living sister animal was allowed to give rise to a culture which was then tested for mating type. In 52 pairs of the 54 so tested, including the 22 which had been shown by individual tests to consist, when mating, of two animals of opposite type, the cultures from the two members of a pair both reacted as type I only. The two exceptional pairs will be discussed in the next section. Since all individuals finally give rise only to type I animals, it seems clear that they are all genotypically type I.

RATE OF CHANGE OF PHENOTYPE

The rate of change from type II to type I is to some extent variable. This is, of course, true for a single caryonide since, in the first left-over cultures, animals of both mating types are present at the same time. It was also found that some caryonides as a whole completed the change in a shorter or longer time than usual. Thus a number of caryonides were found which, although changed by endomixis from type II to type I, gave rise to no left-over cultures containing conjugants. While conjugation may have been overlooked in a few of these, it seems probable that in most of them the change occurred so rapidly that no type II animals were present by the time the first left-over culture was ready to conjugate.

In other cases, the change appears to have taken a longer time than usual. Thus, as already mentioned, 17 of the caryonides gave rise to a second left-over culture which contained conjugants. Moreover, two other caryonides appear to represent cases of such slow change. Only the first left-over culture of each of these caryonides contained conjugants. A later left-over culture from the isolation line of each reacted solely as type I. In each case, one split pair was obtained from the first left-over culture, and cultures were raised from the two members. In both cases, the culture from one member of the pair reacted solely as type I while the culture from the other member reacted with both types but more strongly as type I. Although the behavior of these two caryonides could be explained in other ways, it seems likely that all the descendants of the type II members of

these split pairs had not yet changed to type I by the time the cultures from them were ready to test. This cannot be demonstrated, however, since no other cultures were obtained from these split pairs.

DISCUSSION

When at endomixis, the genotype changes from type II to type I, there appears to be a lag in the corresponding change of the phenotype. In the first, and occasionally the second, left-over cultures derived from the daily isolation lines of these caryonides, there were found to be not only some animals which had changed to type I but also others which were still type II. However, these type II animals gave rise only to cultures which were composed entirely of type I animals. Therefore, the caryonides were genetically type I; and the presence of type II individuals in the early left-over cultures is in all probability due to a lag in the change of the old phenotype.

Such a lag in the change of phenotype following changes of genotype has been reported previously for Paramecium by SONNEBORN and LYNCH (1934) and by DEGARIS (1935). These investigators studied this matter in connection with changes of genotype occurring at conjugation. The two members of a pair of conjugants were found to be alike in genotype following conjugation. However, if the two members of a pair differ in their characteristics before conjugation, it was found that for a time after conjugation they likewise differ but that they gradually approach the common characteristics determined by their like genotypes.

SONNEBORN and LYNCH (1934) working on *Paramecium aurelia* reported such delayed changes for the characters, fission rate and body length. They found that the whole process took from 5 to 14 days in the case of fission rate and from 5 to 8 days in that of body length. Much as in the case reported here, the rate of change varied from clone to clone and was not always the same for two lines of a single clone.

DEGARIS (1935) reported similar phenomena in *Paramecium caudatum* with the character body length. However, he found that the lag period was either lacking or, in some cases, present but very brief for the character fission rate.

Similarly in the present work, no lag period could be detected for a number of caryonides which had changed from type II to type I; and none was ever found for the change from type I to type II. It must be remembered that there was a period of two or three days between endomixis and the time when the first left-over culture was ready to conjugate during which it has not been possible to make studies of mating type. The change of phenotype, then, would not have to be instantaneous in order that no lag in it be found.

Such delayed changes of phenotype have also been reported for Metazoa. TOYAMA (1913) reported that in the silkworm moth, *Bombyx mori*, the color of the egg is determined in some cases by the genetic constitution of the mother although the structure that is colored (the serosa) has the new hybrid genetic constitution.

Both BOYCOTT and DIVER (1923) and STURTEVANT (1923) have interpreted the former's data to show that in the snail *Limnea peregra*, the direction of coiling of the shell is dependent on the genetic constitution of the mother. DIVER, BOYCOTT, and GARSTANG (1925) on the basis of further evidence confirm this interpretation although they show that certain complicating factors are involved.

REDFIELD (1926) reports a lethal effect in *Drosophila melanogaster* that is determined by the genetic constitution of the mother. This lethal kills in the egg stage a considerable part of the female progeny of a female homozygous for the gene involved but has no appreciable effect on the male progeny. REDFIELD thinks that this maternal effect may be due either to an effect on the egg of its unreduced chromosome constitution or to an indirect influence impressed on the egg from without by the mother either before or after reduction. If this last possibility is the correct one, this would not be a case of a lag in the change of phenotype. However, if the first is correct, it would clearly be one.

SEXTON and PANTIN (1927) report a clear case of such a lag in phenotypic change in the crustacean, *Gammarus chevreuxi*. They found that when a female homozygous for the mutant gene "white," was crossed to a male carrying the gene "new red," all the offspring were at first white but later all or half of them become red in color depending on whether the "new red" male was homo- or heterozygous. Similar cases were found with certain other mutant genes.

STURTEVANT (1929) reported that homozygous claret females of *Drosophila simulans* produced a large percent of gynandromorphs and other abnormalities due to irregularities in chromosome behavior both at maturation and during early cleavage. Claret males and heterozygous claret males and females produce no such large percent of abnormal offspring. It thus appears that the effects of the homozygous claret condition in the unreduced eggs last over into the early cleavage stages.

Thus it appears that the occurrence of a time lag in the change of phenotype following changes of genotype is a widespread phenomenon. Cases have been found in such distantly related groups as the Protozoa, the Mollusca, and the Arthropoda.

SONNEBORN and LYNCH (1934) have pointed out two factors that might be the physical basis of the delayed change in phenotype in Paramecium: continued activity of the old macronuclear fragments and delayed change

of the old cytoplasm under the action of the new genotypic constitution. While DEGARIS (1935) does not go into this matter in as much detail as SONNEBORN and LYNCH, he does suggest that the cytoplasm is involved perhaps under the influence of the old macronuclear fragments. The present evidence does not furnish any basis for a decision between the two alternatives.

SUMMARY

1. In the ciliate protozoan *Paramecium aurelia*, a lag in the change of phenotype following a change of genotype from mating type II to mating type I was found after endomixis.

2. In the early left-over cultures of caryonides that had been changed from type II to type I, conjugation was found; and it was shown that type II as well as type I animals were present.

3. Later left-over cultures, however, contained only type I animals.

4. These caryonides were clearly genetically type I since not only type I but also type II individuals from the early left-over cultures gave rise only to type I animals.

5. The rate of the change of phenotype varied for different caryonides and for different animals of the same caryonide.

6. No such lag was found in cases of change from type I to type II and also not in some cases of change from type II to type I, possibly because it was too short to be detected.

7. Similar cases of a lag in the change of phenotype have been found following genetic changes at conjugation in Paramecium. Certain types of maternal effects in Metazoa seem to be the same sort of phenomenon.

8. The physical basis of the lag in the change of phenotype in Paramecium could be either a continued activity of the old macronuclear fragments or a delay in the change of the old cytoplasm under the action of the new genotype.

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RECENT LINKAGE STUDIES IN MAIZE

MAIZE GENETICS COOPERATION
Ithaca, New York

Received October 13, 1938

MAIZE geneticists in different parts of the United States and in other countries have been cooperating very closely with each other since 1932 through the Maize Genetics Cooperation. In addition to freely exchanging seed stocks through the central repository, they freely exchange new methods, hypotheses, suggestions, and unpublished linkage data by means of an annual circular letter. This mimeographed Co-op News Letter does not constitute publication and none of the material in it may be quoted except by permission of the author.

The rapid progress in the genetics of maize may be largely attributed to this liberal exchange of unpublished material among maize workers. Some of the linkage data presented in the Co-op News Letter, however, are complete and should be published so that they will be more readily available to other geneticsts. It is hoped that a group of short linkage papers can be published collectively each year in the same manner as they are presented in this article. Each paper must be considered a separate entity and any reference to the data in it must include the name of its respective author.

For further information on the genetics of maize the reader is referred to "A Summary of Linkage Studies in Maize," Cornell Memoir 180, June, 1935.

I. Virescent seedling-16 (v_{16}).

H. K. HAYES and M. S. CHANG, Minnesota Agricultural Experiment Station.

A virescent seedling in Minn. #13 corn was found to be linked with japonica and given the symbol v_{21}. RHOADES (Co-op News Letter, March 23, 1937) has found v_{16} and v_{21} to be allelic after trisomic tests had placed v_{16} also in chromosome VIII. Further linkage data of *j*, ms_8 and v_{16} are as follows:

GENES *XY*	LINKAGE PHASE	NUMBER OF INDIVIDUALS*					RECOMBINATION PERCENTAGE
		XY	*Xy*	*xY*	*xy*	TOTAL	
J_1V_{16}	*RB*	82	565	542	71	1260	12.1±0.9
J_1V_{16}	*RS*	354	149	154	4	661	16.9±3.7
J_1Ms_8	*CS*	464	39	23	135	661	9.5±1.2
Ms_8V_{16}	*RS*	337	150	171	3	661	13.9±3.8

* Dr. F. R. Immer supervised the taking of these data.

The order of the genes appear to be v_{16}–ms_8–j.

(Paper No. 1510 of the Journal Series of the Minnesota Agricultural Experiment Station.)

II. Zebra striped-6 (zb_6).

H. K. HAYES and M. S. CHANG, Minnesota Agricultural Experiment Station.

Emerson et al. list five cases of zebra striping that have been reported. There are two types, one that is expressed in the seedling stages and which may completely disappear as the plants approach maturity and the other that first appears in partly grown plants. The type reported here was obtained from an inbred line of Del Maiz sweet corn furnished by J. D. BARNARD of the Minnesota Valley Canning Company. The season in 1936 was very hot and dry. Germination of sugary seeds was much lower than normal. Zebra striping could not be classified until late summer when the weather was cooler. Classification was difficult in some cultures. The results given in the summary indicate Zebra striped is located in group 4.

GENES *XY*	LINKAGE PHASE	NUMBER OF INDIVIDUALS					RECOMBINATION PERCENTAGE
		XY	*Xy*	*xY*	*xy*	TOTAL	
Zb_6Tu	*CS*	410	64	64	90	628	23.3±2.0
Zb_6Gl_3	*RS*	326	148	135	19	628	33.9±3.5
TuGl_3	*RS*	314	160	147	7	628	20.5±3.8
Zb_6Su_1	*CS*	4227	259	175	361	5022	13.3±0.5

The order of the genes appears to be su_1–zb–Tu–gl_3.

(Paper No. 1510 of the Journal Series of the Minnesota Agricultural Experiment Station.)

III. Zebra seedling-4 (zb_4).

H. K. HAYES, Minnesota Agricultural Experiment Station.

Zebra seedling, zb_4, has been located in chromosome 1 by the following studies:

GENES	PHASE	*XY*	*Xy*	*xY*	*xy*	TOTAL	PERCENTAGE RECOMBINATION
Zb_4Br	*RS*	448	142	152	12	754	31.1
Zb_4F_1	*RS*	455	135	158	9	757	28.0
Zb_4Bm_2	*RS*	487	103	144	23	757	46.0
Zb_4P	*CS*	266	24	5	64	359	6.9

Progeny of one ear indicated that the *P* parent was heterozygous, giving the following segregation:

CS	63	30	2	24	119	6.7

(Paper No. 1510 of the Journal Series of the Minnesota Agricultural Experiment Station.)

IV. Ramosa ear-2 (*ra*$_2$).

H. K. HAYES, Minnesota Agricultural Experiment Station.

A culture of *ra*$_2$ received from Dr. BRINK at Wisconsin proves to be similar to the one I have studied for many years. There is some variability in type of ear, some cultures showing rudimentary male flowers on the tips of some ears, irregularity of rows on the cob but no division of the cob as in *ra*$_1$. Other cultures have a divided cob on the tip of the ear but a solid cob at the basis. *Ra*$_1$ can be separated from *ra*$_2$ in the F_2 of a cross.

(Paper No. 1510 of the Journal Series of the Minnesota Agricultural Experiment Station.)

V. Opaque endosperm-2 (*o*$_2$).

W. RALPH SINGLETON, Connecticut Experiment Station, New Haven.

Opaque endosperm is a character in which the endosperm has very little or no corneous starch. It is phenotypically indistinguishable from floury. Opaque, however, gives 25 percent recessive seeds on segregating ears, while floury gives the gametic ratio of 50 percent. Classification of opaque is good in flinty stocks. Separation can be facilitated by placing over a light. Normal seeds are translucent while the recessives are opaque. Opaque 2 is located on chromosome VII, probably beyond *v*$_5$, as is shown by the following data. (Opaque 1 has not yet been located in any linkage group.)

Linkage of *o*$_2$, *ra*$_1$, *gl*$_1$, and *ij*:

GENES	PHASE	*XY*	*Xy*	*xY*	*xy*	TOTAL	NO.	PERCENT
O$_2$*Ra*$_1$	*RB*	116	597	554	109	1376	225	16
O$_2$*Ra*$_1$	*CB*	127	15	15	112	269	30	11
O$_2$*Gl*$_1$	*RS*	3148	1595	1487	64	6294		20
O$_2$*Ij*	*RS*	405	169	184	30	688		37

A three-point test involving *o*$_2$, *gl*$_1$, and *ij* gave the following counts:

F_1 GENOTYPE	0	1	2	1, 2	TOTAL
o$_2$ + +	467 513	115 150	94 123	28 23	1513
	980	265	217	51	
+ *gl*$_1$ *ij*		17.5%	14.3%	3.4%	

The recombination percentages of *o*$_2$ and *ra*$_1$ (repulsion phase), also *o*$_2$ and *gl*$_1$ indicate that *o*$_2$ is to the left of *v*$_5$ and within 2 or 3 units of *v*$_5$. The percentages between *o*$_2$ and *ij* indicate that *o*$_2$ is 2 or 3 units to the right of *v*$_5$

VI. White sheath-3 (ws_3).

M. M. RHOADES, U. S. Department of Agriculture, Washington, D. C.

The recessive mutant character white sheath$_3$ is characterized by the partial absence of chlorophyll in the culm and sheaths of the plant. The character can be readily classified both in the seedling and in later stages of development. The expression of the white sheath character is determined by a single recessive gene which has been designated ws_3. It is not allelic with the ws_1 and ws_2 factors reported by KEMPTON (1921) and CLARK (1932). The ws_3 gene was first placed in chromosome II by trisomic tests. Linkage data to be presented here confirm this location. F_2 data from the selfing of $\frac{ws_3 \quad lg_1 \quad Gl_2}{Ws_3 \quad Lg_1 \quad gl_2}$ plants are as follows:

GENES	LINKAGE PHASE	NUMBER OF INDIVIDUALS					RECOMBINATION PERCENT
		XY	*Xy*	*xY*	*xy*	TOTAL	
Ws_3Lg_1	*CS*	1593	103	114	431	2241	11
Ws_3Gl_2	*RS*	1167	529	505	40	2241	27
Lg_1Gl_2	*RS*	1158	549	514	20	2241	19

The order is ws_3–lg_1–gl_2.

The linear order, with the intervening crossover percentages of the genetic factors in chromosome II as determined from the summary of data in EMERSON, et al (1935), is lg_1 19 gl_2 19 *B* 7 *sk* 12 fl_1 6 ts_1 8 v_4. MCCLINTOCK (1931) has shown that both lg_1 and *B* lie in the short arm of chromosome II with lg_1 occupying a more distal position. Studies of a reciprocal translocation involving chromosomes II and V (RHOADES, 1933) indicate that ts_1 is very close in terms of crossover units to the spindle fiber attachment region of chromosome II. Since the data presented here show that ws_3 is to the left of lg_1, which has been placed cytologically near the end of the short arm, it follows that ws_3 lies close to the distal end of the short arm. The map distance from ws_3 to ts_1 is 74 units. There is an unknown amount of crossing over between ws_3 and the distal end of the short arm so this value represents an estimate of the minimum length of the short arm of chromosome II. The length of the long arm of chromosome II used in these studies is 1.4 times that of the short arm. If the assumption is made that the amount of crossing over per unit of physical length is of the same order in the two arms it is possible to arrive at the estimate of 178 units as the total length of the genetic map of chromosome II. This estimate is in all likelihood less than the true map length of this chromosome but may closely approximate it.

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ABSTRACTS OF PAPERS PRESENTED AT THE 1938 MEETINGS OF THE GENETICS SOCIETY OF AMERICA

RICHMOND, VIRGINIA, DECEMBER 28–30, 1938

E. W. LINDSTROM, *Secretary*
Ames, Iowa

ANDERSON, R. L., and WHITING, P. W., Johnson C. Smith University, Charlotte, N. C. and University of Pennsylvania, Philadelphia, Pa.: *Present status of linkage groups in Habrobracon.*——Alleles and linked genes with direction right or left undetermined are given in parentheses following symbols. The X-linked group with map distances is *Sk*-13-*r*(r^s)-17-*gl*-38-*fu* (-10-X)-22-*sb*(sb^s). Orange group is *o*(o^1, o^d, o^i)-11-*m*-28-*k*(k^s, k^e). Small-wings group is *cp*-16-*sv* (-23-*ld*-27-*ma*)-24-*sw*. Red group is *gy* (-4-*ac*-4-*el*)-40-*rd*-34-*ct*. White group is *wh*(wh^e)-10-*st*. Cantaloup group is *bl*-27-*le*-11-*c*-15-*l*-3-*n*-13-*ho*-9-*vl*-5-*cw*-15-*ro*-12-*bu*-37-*cr* (-15-*dr*) -40-*sl*-0-*co*. Data suggest that cantaloup group (187 units) may be loosely linked with red and with white but results are contradictory (translocations?). There is interference in regions *Sk* to *gl* of X group and *le* to *vl* of cantaloup group, but mortality differences make exact determinations unreliable.

BERGNER, A. D., AVERY, A. G., and BLAKESLEE, A. F., Carnegie Institution of Washington, Cold Spring Harbor, N. Y.: *Sectorial chimeras, chromosome deficiencies and doubling of chromosome number in Datura stramonium induced by colchicine treatment.*——Over 2,000 plants were recorded from seeds treated for 3 to 8 days with 0.2 and 0.4 percent colchicine. From higher dosages from 50 to 75 percent were abnormal (mostly plus or minus 4n) of which nearly half show one to four aberrant sectors. Nearly 200 cytological determinations have been made from selected off-type diploids, tetraploids or higher polyploids. Among "diploids," seven types had 2n-1 chromosomes. Among over 100 "tetraploids" (4n=48) the count went as low as 42; one third had 47 chromosomes; one fifth had 46. In tetraploid Daturas there are 12 sets of four chromosomes each. In 46 or less-than-46 chromosome types, one or two chromosomes may be missing from the same set. No set was found with less than two chromosomes. Among 46 chromosome types, 11 showed two chromosomes missing from a single set and 2 showed one chromosome missing from each of two sets. Apparently chromosomes are frequently eliminated before doubling takes place. Such "tetraploid" plants should give partial disomic inheritance. That elimination of chromosomes also follows doubling is shown by the large number of 47 chromosome types as well as the loss of univalents in some of the less-than-47 chromosome types. The largest chromosome appears most frequently eliminated. Higher numbers ranged from 56 to 96. Two types showed a chromosome fragment, one with 47 and one with 45 additional chromosomes.

BLAKESLEE, A. F., WARMKE, H. E., and AVERY, A. G., Carnegie Institution of Washington, Cold Spring Harbor, N. Y.: *Characteristics of induced polyploids in different species of Angiosperms.*——Through treatment with colchicine, 65 different kinds of flowering plants have been induced to double their chromosome numbers. They represent 41 species, 24 genera and 14 families. Among them are 3 sterile species hybrids, which have been transformed into fertile pure-breeding double diploids by doubling their chromosome number. A series of photographs will show the characteristic features of tetraploids in distinction from diploids in respect to size and shape of pollen, seeds, stomata, leaves, floral organs, etc. In general tetraploids are more robust than diploids but in some species the differences are slight. In most species flower size is greater in tetraploids but in some species tetraploids and diploids cannot be distinguished by flower size alone.

BUCK, JOHN B., Department of Embryology, Carnegie Institution of Washington, Baltimore, Md.: *On the origin of chromosome rearrangements.*——If two synapsed homologous chromosomes are coiled into a helix, a break cutting two coils (four strands) divides the chromosome into six fragments which can rejoin two-by-two in 105 different ways. These recombinations result in a large number of diverse translocations, deletions, duplications, inversions, ring-chromosomes, etc. If the synapsed chromosomes be considered as sister chromatids instead of homologs, recombination following breakage in the coiled condition offers a reasonable explanation of the "reversed repeats" found in salivary gland chromosomes.——If a single coiled chromosome is considered to break at contiguous spots in four adjacent coils, 105 recombination chromosomes may be formed which include single, mutually exclusive double, "included" and "overlapping" inversions of one, two or three segments similar to those described by DOBZHANSKY and STURTEVANT in the phylogeny of *Drosophila.*——The principal feature of the coiled-chromosome breakage theory is that it provides a reasonable explanation of how rearrangements apparently requiring two or more simultaneous breaks at widely separated points in the chromosomes can actually be brought about by one break.

BURDETTE, WALTER J., University of Texas, Austin, Texas: *Tetraploid regions in the chromosomes of Drosophila melanogaster.*——Using translocations to chromosome IV, homozygous overlap individuals were obtained for each of 5 regions in the X chromosome and one chromocentral region of the third chromosome. An additional tetraploid region was produced by obtaining a J-shaped chromosome in the homozygous condition. This chromosome originally occurred as a result of the crossing over of the right portion of T(1;4)A-13 with an attached X chromosome to the right of *car*. In 5 other regions tested no homozygous overlap individuals occurred.——The only constant phenotypic effect observed is reduction in size of the ovary. Individuals which are tetraploid for the region between T(1;4)A-w^{M5} and T(1;4)A-9 have rough eyes. The effect of the homozygous overlap condition on viability and fertility is not proportional to the length of the overlap region. Viability and fertility are not

affected to the same extent. The relationship of the viability and fertility between the wildtype, the heterozygous overlap, and the homozygous overlap is not constant for the cases under consideration.

CARLSON, J. GORDON, University of Alabama, University, Ala., and Carnegie Institution of Washington, Cold Spring Harbor, N. Y.: *Mitotic behavior of chromosome fragments lacking spindle attachments in neuroblasts of the grasshopper.*——In their mitotic behavior X-ray induced chromosomal fragments, which lack spindle attachments, resemble unaltered chromosomes in several respects. (1) They lie in the equatorial plane at metaphase. (2) Their "chromatids" begin to separate at anaphase at the same time as do those of the unaltered chromosomes. (3) Their "chromatids" come into intimate contact with the spindle—later, however, than the chromatids possessing spindle attachments. (4) Sister "chromatid" fragments usually move toward opposite poles behind the unaltered chromosomes, and so are included in different daughter cells at telophase. These facts have a bearing on certain hypotheses of the mechanism of mitosis. They demonstrate that the spindle is not essential to the location of the chromosomes in the equatorial plane and to the initial anaphase separation of chromatids and that the movement of sister chromatids into different daughter cells is not entirely dependent on a spindle attachment locus. In one embryo 17 percent of the fragments were included in the cell nucleus with the unaltered chromosomes at telophase and 83 percent came to lie in small accessory nuclei. Sixty percent of the former and 30 percent of the latter showed connections with chromosomes inside the cell nucleus possessing spindle attachments. This suggests delayed reattachment.

CHASE, HERMAN B., University of Chicago, Chicago, Illinois.: *Dominance in the E series of the guinea pig.*——The problem of dominance is of special interest in multiple allelic series. In the black extension series, *E* is the factor for black, e^p for tortoise shell (black and yellow coat), and *e* for yellow. *E* is completely dominant over the lower alleles. Tortoise shells have been tested by matings to yellows (*ee*) to determine if they are homozygous or heterozygous for e^p. The ranges of 34 possible homozygotes and 71 heterozygotes overlap greatly as shown by percentages of colored hairs that are yellow, e^pe^p from 0.0 to 74.1 percent and e^pe from 0.0 to 83.1 percent. Since white spotting affects the black-yellow coat, self animals will be considered alone. *SS* selfs and *Ss* selfs did not differ significantly. Of 115 self animals, tests have been made of 59; 23 are probably e^pe^p and 36 are e^pe. Considering amounts of segregated yellow (clear yellow areas on the coat not mixed with black hairs), e^pe^p has significantly less, 11.3 ± 2.8, a difference of the means (5.2 and 16.5 per cent) which is 4.0 times the standard error. Considering the percentage of hairs which are yellow, the difference between the means (15.1 and 33.2 per cent) of e^pe^p and e^pe is 4.6 times the standard error. The dominance relationships in the black extension series of the guinea pig are then *E* dominant over e^p and *e*, e^p not completely dominant statistically over *e*. Incomplete dominance would be expected if e^p had a mere quantitative effect.

CLARK FRANCES J., Connecticut Agricultural Experiment Station, New Haven, Connecticut, and University of Missouri, Columbia, Mo.: *A gene for abnormal meiotic spindle formation in maize.*——The F_2 of a cross of an untreated female by a male whose sperm (pollen grain) had received unfiltered ultraviolet radiation segregated a number of plants with an atypical spindle formation in the first meiotic mitosis. Meiosis proceeds normally until mid-anaphase I. At this period the dyad chromosomes composing each anaphase group do not converge in a polar cluster. Telophase I cells are produced with several small nuclei, each containing one to several chromosomes. The formation of these multinucleate cells is correlated with a lack of convergence of the spindle substance at its two poles. Instead of converging, the poles of most of the spindles diverge with the chromosomes following the divergent paths. At the second division the several nuclei in each cell produce separate spindles, variously oriented, resulting in a variable number of spores with different numbers of nuclei. Spores with at least a complete set of chromosomes, although in several separate nuclei, are capable of apparently normal growth and can undergo the first microspore division. A single tube nucleus and a single generative nucleus may result from a multinucleate spore through a directed orientation of the several spindles produced by separate nuclei. Some spores, however, show more than one nucleus in each cell after this division. Pollen abortion is 30–60 percent. The character is inherited as a simple recessive.

DEMEREC, M., and HOOVER, MARGARET E., Carnegie Institution of Washington, Cold Spring Harbor, N. Y.: *Hairy-wing duplication in Drosophila melanogaster.*——A salivary gland chromosome study showed that the material carrying the dominant X chromosome gene Hairy-wing has the band designated on BRIDGES' 1938 map as 1B1·2 represented twice. Genetic tests revealed that duplications for that region of the chromosome show the hairy-wing effect although the Hairy-wing gene is not present. This evidence suggests that Hairy-wing is a duplication for a single band.——Data on the number of extra hairs in various combinations of Hairy-wing, wild type, deficiency and duplication for tip sections indicate a similar relationship for this duplication as observed by STURTEVANT for Bar, namely, that the extra gene is more effective if present in two doses in one chromosome than if present in two separate chromosomes. Cytological and genetic evidence suggests that the band representing achaete is duplicated in Hairy-wing. The achaete mutant reduces the number of bristles and hairs, while if our indication proves correct, a duplication for the same locus produces just the opposite effect.

DICE, LEE R., University of Michigan, Ann Arbor, Mich.: *The effectiveness of adverse selection.*——Adverse selection against a recessive is most effective when the homozygous recessives constitute a considerable proportion of the population. As the proportion of homozygous recessives decreases the effectiveness of adverse selection also decreases, but at a much slower rate. The expected reduction in defectives is slightly over 2 percent per generation when

the homozygous recessives constitute only 10 per 100,000 population. Defective characters inherited through sex-linked factors, dominant factors, or factors lacking dominance respond much more readily to adverse selection than do recessive characters.

DOVE, W. FRANKLIN; University of Maine, Orono, Maine: *Not by genes alone.*——An attempt is made to reinterpret the genetics of growth, disease resistance, longevity and efficiency in the utilization of food, in terms of *nutritional behavior*. This method of experimentation (Amer. Nat. **69**) succeeds again in differentiating genetic modifiers from those of a psychological or of an economic nature. It is found that psychological factors such as imitation, dominance-submission, social facilitation and greed versus need, affects, significantly, the phenotypic expression through the medium of nutritional behavior. However, the principal modifier of biological functioning, extraneous to genes, appears to be the *socioeconomic system* as it aids or interferes with the *mode of production* and the *method of distribution* of the food required for the optimum genetic expression sought by the geneticist and the eugenicist as "superior germ plasm."——At present, without an economics of production-for-use, superior germ plasm quickly reverts to "scrub" germ plasm . . . especially in outlying, marginal and soil-depleted regions. Here, genes are submerged by economic factors. Under these circumstances, the search for "superior germ plasm" should be redirected toward the establishment of an economic basis upon which superior germ plasm may thrive.——Observation on the nutritional behavior of phenotypically superior individuals indicates certain economic adjustments necessary for the sustenance of group superiority. An important economic adjustment and a clue to the maintenance of group phenotypic superiority is indicated by the aggridant (the superior type integrated from the group) as an adoption of the bioeconomic Specialization-Diversification Pattern. Through encouragements or pressures, the S-D patterns of the aggridant could be applied to food-production programs so as to ensure an economic and environmental milieu for the support of an otherwise elusive "superior germ plasm."

DUNHAM, H. HOWARD, and REID, W. MALCOLM, Brown University, Providence, R. I.: *Colchicine treatments on Daphnia longispina.*——Parthenogenetic eggs of Daphnia were treated by the addition of colchicine solution to the manure infusion medium used for culture. Daphnia eggs develop in an open brood chamber exposed to substances in the medium.——Concentrations of colchicine ranged from 10^{-4} to 10^{-7} by weight. In different experiments adult mothers were treated before, during, and for one-half to three hours after egg-laying. One hundred seventy-nine mothers treated in seven separate experiments yielded a total 1,317 living young all of which were studied in parallel with control animals of the same age. Of these 1,317 animals (all females) 28 were completely sterile and five were mutants.——Of these five mutants three were remarkably similar in morphological peculiarities. A study of growth, reproduction, and longevity of two of these three has shown them to be prob-

ably identical. Each of the other two mutants was peculiar with respect to myrphology and physiology. In all five cases viability, growth, reproductive activity, size, general vigor and length of life are less than for the parent clone (BANTA's line 1284). Cytological studies have not been made but the remarkable resemblance between three of these five derived clones suggests the possibility of tetraploidy in these three cases.

DUNNING, W. F., and CURTIS, M. R., Columbia University, New York, N. Y.: *Linkage in rats between factors determining a pathological condition and a coat color.*——Death from internal hemorrhage occurred in a number of rats of a pink-eyed dilute inbred line. The pathological condition was characterized as a ruptured thrombosed varix usually in the liver and rarely in the lungs. Thirty F_1 rats derived from crosses between affected pink-eyed rats and normal black-eyed rats resembled their black-eyed parent and did not develop the vascular lesion. Among the F_2's, 3 percent of the 93 black-eyed rats and 26 percent of the 31 pink-eyed dilute rats died with hematomas.

EATON, O. N., and SIMMONS, V. L., U. S. Dept. Agr., Washington, D. C.: *A genetic study of milk goats with especial regard to the occurrence of hermaphroditism.*——Although hermaphroditism occurs more frequently in goats than in any other farm animal, very little data on its frequency is available. Records of the U.S.D.A. herds of Saanens and Toggenburgs since 1925 show 38 hermaphrodites among 343 kids in the former breed and 21 among 350 in the latter. A study of individual matings shows that only certain bucks and does produce intersexes, and in these matings the ratio of normals to hermaphrodites does not depart significantly from 3:1 (20.6 percent hermaphrodites). For both breeds combined, the percentages of young born as singles, twins, and triplets are 16.1, 61.2, and 22.2 respectively. One set of quadruplets was born during the period studied. There is a tendency for more hermaphrodites among triplets than in single or twin births. Hermaphrodites occur with both male and female litter mates. In the Saanen herd the sex ratio was 54 percent males to 46 percent females; in the Toggenburgs it was very nearly 50 percent of each sex. The weight of kids at birth is nearly equal for both breeds and is strongly dependent on number born. The percentage of triplets increases slightly as the age of dam increases. Since the part of endocrines in sex modification must be recognized, the genetic factors concerned with hermaphroditism must act on the gonads during embryonic sexual differentiation in order to produce their effect. Elimination of animals which have produced hermaphrodites from the breeding herd should check the occurrence of hermaphroditism should the single recessive factor theory prove true by further investigation.

EMMONS, C. W. and HOLLAENDER, ALEXANDER, Divisions of Infectious Diseases and Industrial Hygiene of the National Institute of Health and Washington Biophysical Institute, Washington, D. C.: *The influence of monochromatic ultraviolet radiation on the rate of variant production in Trichophyton mentagrophytes.*——*Trichophyton mentagrophytes*, a dermatophyte classified among the Fungi Imperfecti (no sexual stage known), can be considered as

typical of the less highly developed fungi. It produces uninucleate spores, which, in this investigation, were isolated from the multinucleate cells of the microorganisms, and exposed to measured quantities of monochromatic ultraviolet radiation. By random sampling and transfer of germinated spores to agar slants it was found that some of the spores surviving radiation had been so altered that heritable differences from the parent type appeared in cultures. The variants produced by the radiation can be roughly separated into four groups. All of these types differ from the variant commonly appearing in old cultures ("pleomorphic" growth) and are easily distinguishable from abnormal colonies due to adverse growth conditions. The uniformity of consecutive subcultures of normal strains of dermatophytes when properly cared for, and the apparent permanency of the variants induced by ultraviolet radiation indicate that under controlled environmental conditions colony form, growth rate, and pigment formation are inherited characters of genetical importance.

EYSTER, WILLIAM H., Bucknell University, Lewisburg, Pa.: *Interspecific hybrids in Tagetes.*——The diploid chromosome number of *Tagetes erecta* is 24, that of *T. patula* 48, and their interspecific hybrid 36. These chromosome differences are indicated by differences in pollen size and the high degree of sterility of the hybrids. Although the hybrids are intermediate between the parent species in plant habit, size and color of flower heads, and leaf characteristics, they are like one or the other parent in the structural characteristics of the disk and ray florets respectively.

FANKHAUSER, GERHARD, Princeton University, Princeton, N. J.: *The effects of triploidy on cell size and organ size in salamanders.*——Occasional triploid larvae of the newt, *Triturus viridescens*, occur in nature. These may be identified among living larvae by chromosome counts in amputated tailtips. Last winter, four triploid individuals were raised to an age of $3\frac{1}{2}$ to 4 months, and preserved during or after metamorphosis. Three of these were not significantly larger than diploid controls, while the fourth showed signs of gigantism from an early larval stage on (FANKHAUSER 1938).——The comparison of serial sections through the triploids and controls shows that the triploid nuclei and cells are, on the average, definitely larger than the diploid in all organs and tissues that have been investigated so far (spinal cord, spinal ganglia, notochord, cartilage from pelvis and skull, liver, intestine, kidney, lingual glands). The number of cells, on the other hand, is reduced in most organs, so that the total size of the organs is about the same as in diploid individuals in the first three triploids, slightly larger in the fourth. The notochord alone appears to be considerably larger in all triploids.——The observations demonstrate that the organism may compensate the larger size of the triploid cells by a corresponding reduction in cell number, keeping the size of the organs and body within approximately normal limits. The presence of such a regulating mechanism in a vertebrate is in disagreement with HEILBORN'S and DARLINGTON'S suggestion that the harmful consequences of a heavy increase in organ size might account in part for the scarcity of polyploidy among animals.

FERGUSON, MARGARET C., Wellesley College, Wellesley, Mass.: *The inheritance of color-pattern in the corolla-limb of two strains of Petunia, and in their hybrids.*——Population five (P_5) bears dark purple self-colored flowers which occasionally show a tiny white spot *within* the corolla-limb; P_{12} bears deep pink flowers which may show one or more *marginal* white blotches. Each strain breeds true to its characteristic color-pattern. The F_1 hybrids are intermediate in color, and range in different plants, or on the same plant, from self-color to pure white. The F_2's give rise to various colors, but to no greater variation in color-pattern than do the F_1's. This study is concerned with pattern-inheritance, not with the inheritance of color. These plants were introduced into our cultures in 1920. The study covers more than 16,000 plants, and over a half million flowers have been recorded. It is entirely possible to work out a factorial analysis in explanation of the very striking range of variation in the color-patterns of the flowers in these strains and their hybrids. But such an analysis fails to explain satisfactorily why, the original patterns having once occurred, it is apparently impossible to eliminate them, either by selfing the self-colored hybrids or by outbreeding to species homozygous for self-color; or why, when the pure white hybrids are selfed, spotted or even self-colored flowers appear in their progeny. The evidence, when all in, leads one to assume that the conditions are parallel to those which underlie certain human maladies; and that the problem of pattern, individual and racial, is a cellular problem—a problem of the gene and of its intra- and inter-cellular environment.

GOODRICH, H. B. and TRINKAUS, J. P., Wesleyan University, Middletown, Conn.: *The effect of ultraviolet radiation on the color pattern of phenotypes of the goldfish, Carassius auratus.*——The three phenotypes of goldfish used were the common goldfish *TT*, the colorless shubunkin *T'T'*, and the F_1 heterozygous type which is the calico shubunkin. These types were subjected to ultraviolet radiation of restricted areas of the body. The two parental types have few or no melanophores and these showed no reaction to the radiation. The F_1 or calico fish is normally irregularly spotted with groups of melanophores which arise and disappear during the life cycle. This type reacted to radiation by developing a significant excess of new groups of melanophores appearing within the radiated areas in contrast with a relatively smaller number appearing in all other parts of the body. The period of excess frequency of new spots extended over an interval lasting from the end of the 1st to the 8th week after radiation with a maximum at the 5th week. After this period the frequency in the unradiated more nearly approximated that in the treated area. The theory is suggested that the radiation stimulates the development and multiplication of latent chromatoblasts which normally would develop later during the life of the fish.

GOWEN, JOHN W., Iowa State College, Ames, Iowa: *Behavior of tobacco mosaic virus irradiated with X-rays of different wave lengths.*——The gene-like self-reproducing properties and mutating ability of tobacco mosaic virus gives interest to another characteristic, the effect of radiant energy of different wave

lengths on the inactivation rates. These effects are, in contradistinction to genes, uncomplicated by surrounding matrices of other tissues.——*Tobacco mosaic virus* either dissolved in buffer solution or dried on cellophane is inactivated by X-rays at a uniform rate. The water surrounding such material, contrary to the suggestion of some, does not have any indirect chemical or other effects. For irradiation with X-rays of long, copper and medium, silver, wave lengths, the medium wave length is distinctly more effective when ability to ionize air is used as the measurement of dosage.

GRIFFEN, A. B., and STONE, W. S., University of Texas, Austin, Texas: *The demonstration of a new chromosome arm in D. melanogaster.*——There is now genetic and cytological evidence for a second arm for the fourth chromosome in *D. melanogaster* designated as 4L to conform with the scheme of BRIDGES' map (1935). The proof was obtained from a translocation, Tl-4A,18, a white mottled stock, w^{Ma}, with XL through the white locus linked to the fourth chromosome in such a way that in a back cross to eyeless, XL hyperploids are non-eyeless. The break is thus proven to be either distal to the normal allele of eyeless or across the centromere from it. In metaphase plates this XL+4 element appears as a small, distinctly V-shaped body. Salivary gland chromosome analysis shows that XL through 3C2 is attached across the centromere from the normal allele of eyeless beyond the fifth heavy band in 4L.

GRIFFEN, ALLEN B. and STONE, WILSON S., University of Texas, Austin Texas: *Reverse mutation and the position effect.*——Three spontaneous point mutations, apricot, miniature, and forked were induced to reverse to a normal allele by irradiation. In the one case for each thus far studied, genetically and cytologically, there was no detectable gene rearrangement. On the other hand, in each of over forty cases of X-ray-induced reversal or partial reversal of white mottles to a normal allele thus far carefully analyzed, a new gene rearrangement had occurred. If these relations continue to hold as more cases are analyzed, we must conclude that the white mottles studied do not reverse *in situ* to a normal allele by point mutation. As yet we cannot say whether a simple point mutation, spontaneous or otherwise, can revert to a normal allele as the result of a "position effect."

HARNLY, MORRIS HENRY, Washington Square College, New York University, New York City: *Postpuparium development of the wings of the mutants vestigial and pennant of Drosophila melanogaster.*——An inbred stock of vestigial was reared at 32°C until puparium formation. Isolated puparia were transferred to 25°C for further development because 32°C was lethal during the pupal period. From 8 to 18 hours after puparium formation there are no signs of regression of the wing within its sheath. The phenotypes range from an occasional strap to nearly wild-type and were typical of those found on adult flies reared at 32°C. Twenty-four hours after puparium formation approximately 50 percent of the wings showed signs of some regression within the sheath. At 30, 36, and 49 hours after puparium formation, further regres-

sion of the wing within the sheath was found in some cases while in others very little if any regression occurred. There was no correlation between size and shape of the originally everted wing as determined from the sheath and the amount of regression of the wing. Strap wing might develop in a strap shaped sheath with almost no regression or a strap wing developed in a practically wild-type sheath through marked regression and due to its lengthening lie Z-shaped within the sheath. Other nearly wild-type sheaths contained wings showing almost no regression. The legs 36 hours after puparium formation were only a third the diameter of their sheaths. In pennant flies minor regressions of the wings begin at approximately 20 hours after puparium formation at 30°C. The entire series of alleles are being investigated in both pre- and post-puparial stages.

HARVEY, PAUL H., Iowa State College, Ames, Iowa: *Hereditary variation in plant nutrition.*——Corn inbred strains were grown in aqueous mineral cultures supplied with different nitrogen forms and statistical analyses made on the total dry weight of plants (five to six weeks old). Differential strain response to nitrogen forms (nitrate vs. ammonium ion) was demonstrated. Inbreds La and PR consistently produced relatively more dry matter on ammonium nitrogen than did inbreds Mc, Hy, and R4. Single crosses involving these inbreds also responded differentially to the two nitrogen forms. These showed definite parent-offspring correlations with regard to growth on the nitrogen forms. Hybrid response was in general intermediate between that of parent lines. Inbred strains which utilized ammonium nitrogen efficiently had equal percentages of dry matter whether grown on ammonium or nitrate nitrogen. On the other hand, strains which failed to utilize ammonium nitrogen efficiently had lower percentages of dry matter for ammonium-grown than for nitrate-grown plants. This indicates better metabolism of ammonium nitrogen by the former strains than by the latter type. The individuality of corn inbreds was shown by the consistently highly significant differences in top-root ratios between strains. Tomato varieties and strains of two species, *Lycopersicum esculentum* and *L. pimpinellifolium*, responded differentially on high and low levels of nitrogen, phosphorus, and potassium supplied in nutrient cultures. Hybrids of strains most extreme in potassium response were tested and showed clearly the inheritance of the complex responsible for the strain differences. Hybrids of one efficient and one inefficient parent were intermediate in their utilization of limited potassium supply.

HAYS, F. A., Massachusetts State College, Amherst, Mass.: *Breeding small flocks of domestic fowl for high fecundity.*——A foundation stock consisting of 45 pullets and 27 cockerels of the Rhode Island Red breed was used to establish two lines. Line A was selectively bred for exhibition plumage color alone. Line B was selectively bred for characters affecting fecundity without sacrificing desirable plumage color. These two lines were carried through eight generations. The number of pullets housed and trapnested in each line from generation to generation was small, ranging from 13 to 78 with an average of

about 30.——Complete records were obtained on the following: Sexual maturity, weight at first egg, winter intensity, winter egg weight, winter pause, winter egg production, broodiness, persistency, annual egg record and annual mortality. The data make possible a comparison of the two lines and a study of progress or lack of progress in eight generations. The data show rather definitely just why breeding with small numbers accomplishes little.

HOLLAENDER, ALEXANDER, and EMMONS, C. W., Washington Biophysical Institute and Divisions of Industrial Hygiene and Infectious Diseases of the National Institute of Health, Washington, D. C.: *Fungicidal and sublethal effects of monochromatic ultraviolet radiation on the spores of Dermatophytes.*——Spores of *Trichophyton mentagrophytes* (a strain causing "athlete's foot") were irradiated with measured quantities of monochromatic ultraviolet radiation between the wavelengths 2180–3650A in such a manner that each spore received and absorbed with practical uniformity an equal amount of monochromatic radiation during a given exposure. Percentage survival ratio curves were plotted from the data obtained by plate counts. Wavelength dependence curves for 50 percent survival ratio of colony-forming organisms at the wavelengths between 2,280–3,000, the region most thoroughly tested in this investigation, show a definite maximum at 2,650A, and a decreasing sensitivity towards lower and higher wavelengths. The sensitivity of these spores is about 100 times less the sensitivity of typical bacteria and is close to the sensitivity of yeast cells. The first sublethal effect observed was a delay in the appearance of colonies produced by spores surviving irradiation. This is emphasized by the appearance of some colonies of smaller size and very slow growth; this physiological effect disappears in subsequent transfers.——A certain percentage of spores which had survived large amounts of radiation produced colonies which differed from the normal in colony form, color, rate of growth, and spore production. The appearance of these variants was regular, persisted in consecutive transfers, and was most pronounced at certain energy values and wavelengths. The wavelengths most effective in killing, 2,650–2,537, were also most effective in producing these variants. The absorption spectra of possible compounds in the cell nucleus affected by the radiation will be discussed.

HORTON, IRA H., University of Texas, Austin, Texas: *A comparative study of the salivary gland chromosomes of Drosophila melanogaster and D. simulans.*——Ten visible chromosome rearrangements have been found. Six are inversions, five of which are very small, and four involve changes of one or a few bands in the free ends of the X, II L and R and chromosome IV. Homologous bands undergo somatic synapsis even though one is inverted. There is no evidence for the gain or loss of any bands in either species; the extra bands in the X of *D. simulans*, reported by PATAU, are the result of short inversions. There are about fourteen short areas in the long chromosomes which characteristically do not undergo somatic synapsis. In view of the fact that a very short inversion, even of two lines, ordinarily prevents synapsis for some distance to either side of the normal bands it seems probable that most of these fourteen

non-synapsing areas are the result of minute chromosome rearrangements not easily visible in the band pattern. If this interpretation is correct, then there is evidence for 24 rearrangements (23 are very small) since the two species arose from a common stem.

HUNT, H. R., and HOPPERT, C. A., Michigan State College, East Lansing, Mich.: *Inheritance in rat caries.*——The role of inheritance in human tooth decay is a disputed question. The attempt is made here to determine whether inherited differences appear in rats when the food, litter size, age when the caries ration begins, etc. are held constant. The caries-producing ration comprises rice (66 percent, coarsely ground), whole milk powder (30 percent), alfalfa leaf meal (3 percent), salt (1 percent).——119 rats from three sources developed caries from 28 to 168 days after the introduction of the caries diet. Two inbred lines, early and late caries developers, are being formed by mating siblings within each line. Conspicuously susceptible siblings, from fraternities which are uniformly early developers, are selected for mating in the early line. Highly resistant siblings from resistant fraternities are bred in the late line. The third generation of the resistant, and the fourth generation of the susceptible line have been reached. Conclusions would be premature at present. However, family differences within, and between, the two lines are evident. The extremes within the fourth generation of the early line are the appearance of caries 16 and 51 days after the beginning of the caries diet. Corresponding limits for the (nearly completed) second generation of the late line are 35 and 249 days, with sibship averages ranging from 81 to 132 days.

HUSTED, LADLEY, University of Virginia, Charlottesville, Va.: *Chromosome knots in microspores of Paris and Pancratium.*——Knots have been frequently found at mitotic prophase in microspores of Paris, Pancratium, and Tradescantia. In Paris the knots nearly always have the same direction as the relic spiral and the same order of magnitude. Well formed relic spirals are found distal to many of the knots. As the chromosomes shorten and increase in diameter the knots appear to become untied. In a plant of Paris having abnormal microspores (like those experimentally produced by temperature changes) 22 percent of the prophase nuclei contain one or more knots. In plants which have normal pollen knots are found in fewer than 8 percent of the prophases. Their origin is easily explained if it is assumed that the spiralled chromosome breaks and that broken ends unite with broken ends after another portion of the chromosome has pushed through the broken region or a structural change has occurred.

HUSTED, LADLEY, University of Virginia, Charlottesville, Va.: *Chromosome morphology and meiotic association in the flatworm, Mesostoma ehrenbergii.*——*Mesostoma ehrenbergii* was reported from Europe by FOCKE in 1836. Since then the species has been found in Asia, Trinidad, and in five of the United States. The European form has ten chromosomes with approximately median centromeres. In the primary spermatocyte six of these chromosomes form bivalents

and four are present as univalents. The eleven individuals of the American form examined have eight chromosomes. Each pair is easily distinguished from the others. The two shortest chromosomes are ca. 14μ long and the two longest 27μ at mitotic metaphase. These are the largest chromosomes found in American Turbellaria. In the primary spermatocyte three bivalents occur and two chromosomes, always the same chromosomes, remain unpaired.

JONES, DONALD F., Connecticut Agricultural Experiment Station, New Haven, Connecticut.: *Growth changes associated with chromosome breakage and reattachment.*——Growth alterations in maize endosperm occur in the form of raised or depressed areas. These two types of tissue variations may be paired or single. They may or may not coincide with color changes resulting from the loss or shift of known loci. In the paired red and dark spots resulting from the shift of the *Pr* gene, or the white and dark spots resulting from the shift of the *C* gene the raised area may coincide with the red or white area in one case or with the dark area in the other. These changes in the rate of cell multiplication or size are comparatively rare, being found in less than one percent of all the color changes. The evidence indicates that these alterations in cell activity are not a manifestation of the action of the color genes themselves. Neither are they due to shifts of other loci on the same chromosomes, otherwise there would be a higher association of color changes and growth changes. From the evidence at hand they seem to be due either to a chromosomal unbalance that is not lethal or to a physiological change at specific points of chromosome breakage and reattachment.

KAUFMANN, B. P., Carnegie Institution of Washington, Cold Spring Harbor, N. Y.: *The course of abnormal development in eggs of hybrids between Drosophila miranda and Drosophila pseudoobscura.*——These species differ widely in the arrangement of the genic materials in the chromosomes (DOBZHANSKY and TAN 1936). When crossed to each other they produce sterile hybrids. In an effort to determine whether this sterility is of the genic or chromosomal type, meiosis and subsequent developmental stages were studied in eggs of hybrids fertilized by sperm of one of the parental species.——Most of the eggs furnished evidence that the meiotic divisions are carried to completion. Direct observations of chromosome behavior during these divisions are meagre, but in some cases at the termination of meiosis the group of polar nuclei contains 3n chromosome (12 large elements; the dot-like chromosomes are not distinguishable) and the female pronucleus a group of four large chromosomes. This suggests that an occasional female pronucleus should carry a complete set of chromosomes of one of the parental species. Under certain conditions zygotes containing such chromosomes should possess potentialities for continued development unless inhibited by the genetic constitution of the organism. However, an additional complicating factor frequently prevents the occurrence of any considerable number of cleavage mitoses. This is the extensive proliferation of the polar body chromosomes leading either to the formation of numerous scattered bits of chromatin or to a smaller number of large

chromatin masses. In some eggs the zygote nucleus likewise begins a series of aberrant mitoses and abnormal chromosome multiplication. As a result of these processes embryonic degeneration ensues within a few hours of fertilization.

LANGHAM, D. G., Cornell University, Ithaca, N. Y.: *The inheritance of intergeneric differences in Zea-Euchlaena hybrids.*——Although maize and teosinte are listed botanically in separate genera, their characteristic differences are few. The following evidence supports the theory of the evolution of maize from teosinte by mutation.——Extensive F_2 and reciprocal backcross populations show that paired vs. single spikelets, many-ranked vs. two-ranked ear, and weak vs. strong response to length of day are inherited as simple genetic characters. (See also COLLINS and KEMPTON, 1920.) Furthermore, in inbred lines of maize, mutations back to the teosinte characters occur singly. The allelism of these mutant forms of maize with the corresponding teosinte forms has been shown by test crosses with teosinte.——Two prominent theories of the origin of the maize ear are (1) it is the result of the fusion of the lateral branches of the tassel and (2) it represents the central spike of the tassel. Neither view, however, explains the origin of the central spike.——The close relationship of the maize ear and the central spike of the tassel, and their origin by fusion of the two-ranked central branch of the teosinte tassel with one or more lateral branches are indicated by (1) the number of pistillate spikelets on the ear varies directly as the number of staminate spikelets on the central branch of the tassel; (2) maize with the two-ranked ear has the two-ranked central branch; (3) partial fusion often occurs in F_2 populations of maize-teosinte crosses; (4) in segregating populations, two-ranked ear is associated with two-ranked central branch, and many-ranked ear with many-ranked central branch.

LINCOLN, R. E., and LINDSTROM, E. W., Iowa State College, Ames, Iowa: *Micro-evolution of host-parasite interactions in bacterial wilt of maize.*——Experimental material consisted of homozygous, wilt-resistant or susceptible, inbred lines of maize and single-cell isolations of virulent or avirulent strains of bacterial wilt pathogen (*Bacterium stewartii*) which also differed morphologically in colony characters. Two different experimental approaches (1) continuous passage (and reisolation) of pure, virulent or avirulent bacterial strains through resistant or susceptible hosts and (2) inoculation of same hosts with mixtures of virulent and avirulent bacteria of known proportions with later tests for change in this proportion, yielded parallel results. With continuous passage bacterial virulence increased in the resistant and decreased in the susceptible host. Inoculation of mixed cultures in resistant host resulted in an increase in the proportion of the virulent type; through the susceptible host in a decrease of the virulent type. The rate of change of virulence was more rapid in mixed-culture inoculations than in single-cell cultures. Results with first approach can be explained on known genetic rates of mutation and selection; with second approach, on differential selection of parasite in micro-environment of host.

LUCE, WILBUR M., University of Illinois, Urbana, Illinois.: *The effect of a 95 percent oxygen 5 percent carbon dioxide mixture upon facet number in infrabar in Drosophila melanogaster.*——The eggs of an inbred strain of forked infrabar of *Drosophila melanogaster*, in shells vials containing banana-agar-yeast food, were placed in a chamber and treated continuously with a mixture of 95 percent oxygen and 5 percent carbon dioxide for the first 78 hours of development. The chamber was then connected with an air line and air was passed through until the flies emerged from pupa cases. A chamber containing a control set of vials with eggs was treated with air for entire period of development. The experiment was carried out at a temperature of 24 degrees C. $\pm$0.5.——Mean facet number of females treated with the oxygen carbon dioxide mixture was 335.39 $\pm$ 8.74 while that of the controls treated with air was 179.50 $\pm$ 3.19. Exact data on the length of larval stage were not taken. However, the observations that were made indicated that the length of the larval stage for flies treated with oxygen and carbon dioxide was approximately 196 hours while that for the air treated flies was 126 hours. The number of adult flies produced with the O_2,CO_2 mixture was about two thirds that of the controls suggesting a semi-lethal effect of the treatment.——These data suggest the tentative hypothesis, which is being tested by further work, that the O_2,CO_2 treatment retards general development and at the same time in some manner accelerates the processes involved in facet production.

JOHNSON, L. E. and LUSH, JAY L., Iowa State College, Ames, Iowa: *"Legless"—a new lethal in swine.*——Twenty-two legless pigs were born in 1938 among 27 litters of high grade Poland-China swine on an Iowa farm. The pigs were born alive and, except for the legless condition, appeared as healthy and vigorous as their normal litter mates. They lived for two or three days and seemingly died from starvation. None of the limb bones were present in the defective pigs and the scapulae and pelvic bones were not completely formed. The nerves leading to the limbs were present and apparently ended because of the absence of the legs into which to grow. Cleft palate and atresia ani accompanied the defect in some cases. The defect appears to be inherited as a simple Mendelian recessive.

MACKENSEN, OTTO, U. S. Department of Agriculture, Southern States Bee Culture Field Laboratory, University, La.: *Egg viability in the honeybee and its bearing on the problem of sex determination.*——In various tests the egg viability of naturally mated queens averaged 89.7 percent, that of queens artificially inseminated with sperm from a single drone averaged 90.5 percent, while that of queens artificially inseminated with sperm from several drones averaged 60.2 percent. These results can be explained if we assume that the mechanism of sex determination in the honeybee is similar to that suggested by WHITING for Habrobracon. There would then be two types of drones, one producing X-bearing sperm and the other Y-bearing sperm. When a queen is inseminated with only one drone, only one type of sperm can enter the egg (from three to seven enter the honeybee egg) and after differential maturation only highly

viable XY combinations would be possible. When a queen is inseminated with sperm from several drones both X- and Y-bearing sperm can enter the egg making possible frequent XX and YY combinations. If such combinations have a low egg viability as is the case in *Habrobracon*, then the low viability of eggs of queens inseminated with several drones is accounted for.

MARGOLIS, OTTO S., Western Reserve University, Cleveland, Ohio: *The facet distribution in Bar-eyed Drosophila.*——An analysis of data on facet number in two highly inbred stocks of *Drosophila melanogaster* shows that the normal curve of variation may be applied to the facet distributions as a very satisfactory approximation.——The statistical criteria, β, and β_2, approximate the theoretical values of 0 and 3, respectively, in both stocks and for both sexes.——The χ^2 test for goodness of fit calculated for (n-3) degrees of freedom gives probability values of 0.089 and 0.045 for males and females of Stock A, respectively; and 0.204 and 0.265 for males and females of Stock B.——Data on flies raised under crowded conditions show that a marked positive skewness is produced.

METZ, C. W., and H. V. CROUSE, Carnegie Institution of Washington, Baltimore, Md.: *Studies on species hybrids and evolutionary chromosome changes in Sciara.*——Further studies, on individual species and on species hybrids, support observations previously reported indicating that in Sciara gross chromosome rearrangements (translocations, inversions) are rare, and that this may account for very low mutation rate here. Minute chromosome changes, however, are common, in contrast to reverse condition found in Drosophila.——Salivary gland chromosomes are shown illustrating these features, also evidence suggesting localized qualitative (gene?) changes.——Chromosomes of *S. ocellaris* and *S. reynoldsi* differ not only in structure, but apparently also in general physical consistency. Possibly the latter influences rate of chromosome change and is responsible for an apparent difference between the two in response to irradiation.——Ocellaris males copulate as readily with reynoldsi as with ocellaris females; sperm are transferred normally, but no offspring result. The reciprocal mating is secured with difficulty, but offspring are secured —some males fertile, all females sterile. Different strains of ocellaris behave differently in crosses with reynoldsi.——In ocellaris two morphologically different chromosome groups are found in different strains. Bisexual strains thus far all show 4 rods, 2 small V's, 2 large V's. Some "unisexual" stocks show 6 rods, 2 large V's; in others 5 rods, 1 small V, 2 large V's are found. Results of racial crosses are illustrated, with detailed comparison of salivary gland chromosomes. All strains of *S. reynoldsi* thus far are bisexual and show 4 rods, 2 small V's, 2 large V's.——Preliminary evidence suggests that homologous "repeats" are present in X chromosome of these two species and possibly a third.

MURRAY, MERRITT J., Cornell University, Ithaca, N. Y.: *Reciprocal hybrids in the family Amaranthaceae in relation to sex determination.*——Two stable

dioecious species, *Acnida tamariscina* (Nutt.) Wood. and *Acnida cuspidata* Bert. which give normal 1:1 sex ratios when inbred have been crossed reciprocally to three stable monoecious species, *Amaranthus retroflexus* L., *Amaranthus hybridus* L., and *Amaranthus caudatus* L. The F_1 progeny of these intergeneric crosses having the monoecious species as the female parent consists of male and female plants in approximately equal numbers. The reciprocal of these crosses gives only females. Neuter plants, lacking the organs of either sex, arise in the F_1 progeny of certain crosses between *Acnida tamariscina* and any of the three monoecious species. The neuter condition is genetic since it shows almost complete linkage to a color factor present in *A. tamariscina*. Interspecific crosses between the three monoecious species yield only monoecious hybrids. Reciprocal crosses between the two dioecious species give normal 1:1 sex ratios. *Amaranthus spinosus* L., also monoecious, has a different flower arrangement from the three monoecious species listed above. F_1 hybrids between the two types of monoecious flower arrangement indicate that the spinosus type is recessive to the other. When *Acnida tamariscina* as the female parent is crossed to *Amaranthus spinosus* the F_1 progeny are almost all males.

NEEL, JAMES, University of Rochester, Rochester, N. Y.: *Studies on the pattern of supernumerary machrochaetae in Drosophila.*——Five bristle patterns have been studied: normal and Polychaeta in *Drosophila funebris*; normal, Hairy wing, and polychaetoid in *D. melanogaster*. In each of the three mutant patterns, supernumerary bristles (macrochaetae) are present on the dorsum of the thorax. Attention has been centered upon the dorso-central region. Two questions have been investigated: (a) what, with respect to the normal bristles, is the position of the extra bristles, and (b) what is their size?——(a) It can be shown that when only one supernumerary machrochaeta is present, it almost always arises through hypertrophy of some one of the hairs (microchaetae) which are present on normal flies. When several (two or three) extra bristles occur, most of them arise through hair hypertrophy but some are found very close to a normally situated bristle, so that the basal rings are contiguous or almost so, i.e., arise in an area which normally gives evidence of bristle-forming potency. Some few of the supernumerary machrochaetae are found in places which do not normally, either by the presence of hairs or bristles, give evidence of such potencies. There is some interdependence of position, since the appearance of a "new" bristle at one spot may result in a shift in position of an "old" bristle.——(b) The largest bristles are usually found in the position of the normal anterior and posterior dorso-centrals. As distance from these points over the thorax in any direction increases, there is a tendency for bristle size to decrease. This may be interpreted in terms of a gradation of bristle-forming potencies on the thorax.

OFFERMANN, CARLOS A., Academy of Sciences, Moscow, USSR, and University of Chicago, Chicago, Ill.: *Effect of ageing on the frequency of induced mutations.*——To test the relative susceptibility to genetical change of aged germ cells in Drosophila, young and aged flies were simultaneously subjected to

X-ray treatment. The effect was measured by the frequency of lethals in the offspring. The period of aging varied from one to one and a half months. Over 13,000 chromosomes were analyzed. In the first set of tests males and unmated females were aged separately, then irradiated together and also mated with young flies. The induced lethals were found to be almost twice as frequent in old (12.4 percent) as in young (6.8) sperm, the weighted mean difference (5.34 $\pm$1.53) being 3.55 its standard error. No significant difference was observed in the case of old and young females (D=0.42$\pm$1.12; R=0.40X); this is attributed to a more or less continuous renewal of the eggs in in the female. In a second series dealing only with the effect on sperm, treated males mated to young untreated females, gave similar results: 12.32 and 7.03 percent of lethals for aged and young sperm respectively (D=5.29$\pm$1.42; R=3.74X). A third series concerned the time distribution of the age effect: the frequency of induced lethals in sperm aged in females during 0, 12, 24, 36 days, did not show time proportionality, since a significant increase appeared only in the last period. A study of the separate and combined effects of ageing and irradiation on relative sterility shows that sterility is not representative of the direct genetic effects.

OLIVER, C. P., University of Minnesota, Minneapolis, Minn.: *A reversion in Drosophila melanogaster which affected the dominant eye color punch and its recessive lethal.*——Homogeneous punch eye color is connected with a translocation involving chromosomes two and three; three being broken between *h* and *cu*, with the attachment near the right end of two. Reversed-punch, by irradiation, has wild-type eye color at room temperature, and occasionally brownish color at cold temperature. Its viability and fertility are better than those of punch. The translocation is retained. Neither punch nor reversed-punch lives homozygous. Each balances with *CyD*. Matings of *CyD/Pu* males to like females produced only *CyD/Pu* (210). Matings of *CyD/Pu*^{rv} males and females produced only *CyD/Pu*^{rv} (456). Wild type mated to *CyD/Pu* produced 132 *CyD* and 136 *Pu* offspring; wild type mated to *CyD/Pu*^{rv} produced 287 *CyD* and 326 *Pu*^{rv}. Either *Pu/Pu* or *Pu*^{rv}/*Pu*^{rv} is lethal. *Pu/Pu*^{rv} is not lethal, although the form is sterile in either sex. The mutation of *Pu* to wild-type eye color occurred simultaneously with a change of the lethal to non-lethal; a second lethal developed with *Pu*^{rv}. Matings of *CyD/Pu* to *CyD/Pu*^{rv} produced 267 *CyD/Pu*, 278 *CyD/Pu*^{rv}, and 89 *Pu/Pu*^{rv}. The *Pu/Pu*^{rv} have darkened bodies, a definite trident on the thorax, opaque wings occasionally plexate, and in the females roughish eyes. No considerable change has occurred in the chromosomal fragmentations. Both *Pu* and *Pu*^{rv} have similar abnormal crossing over in the right arm of two and left arm of three, with approximately normal crossing over in the other arms.

O'MARA, JOSEPH G., U. S. Department of Agriculture and University of Missouri, Columbia, Mo.: *Cytological observations on Zea-Euchlaena hybrids.*——The intergeneric hybrid *Zea mays* $\times$ *Euchlaena mexicana* has generally been found rather unfavorable material for pachytene cytology, owing apparently to the influence of the *Euchlaena* parent. Ten other varieties of *E. mexi-*

cana (supplied by J. H. KEMPTON) were studied to secure types which could be most effectively used for cytological studies. Those which gave the best pachytene preparations were crossed with a single plant of maize, and in these hybrids, observations were made to determine the extent of homology, and whether the hybrid was favorable cytological material. Among the teosintes from Mexico, all of which had non-terminal knobs, a variety collected at Nobogame yielded favorable pachytene material, and in the hybrid with maize showed apparently complete homology and regular disjunction. The knobs found occurred at the same loci as the corresponding maize knobs, except for a small knob on the short arm of chromosome two. Among the teosintes from Guatemala, all of which had terminal knobs, a variety collected at Nojoya gave excellent pachytene preparations, equal to those of the best stocks of maize. This variety should be of use in cytogenetic studies to which maize is not adapted, since most of the chromosome arms have terminal markers. In the hybrids with maize the pachytene chromosomes show complete homology and disjunction is regular. The heteromorphic homologues found in Florida teosinte-maize hybrids, and described in Durango teosinte-maize hybrids, do not occur in the hybrids between maize and the teosintes from Nobogame or Nojoya.

PIPKIN, SARAH BEDICHEK, North Texas Agricultural College, Arlington, Texas: *Crossing over and disjunction in a II-III translocation in Drosophila.* ——In this mutual translocation, II and III were broken by X-radiation in their chromocentral regions; and the left arm of II, IIL, attached to the right arm of III, IIIR; and IIR to IIIL. Different gamete types occurred with the same frequency in males and females heterozygous for the translocation: (1) regular gametes resulting from distribution of alternate members of the "ring of four" to the same pole, and containing one homologue each of the right and left arms of II and III, 59.06 percent; (2) exceptional gametes, 25.03 percent and 13.41 respectively, according to the two methods by which two adjacent members of the "ring of four" can be distributed to the same pole; and containing one homologue of each of two arms, two homologues of the third arm, and no homologue of the fourth arm of the II or III. The remaining 2.50 percent gametes arise from a three-one distribution of members of the "ring of four." Crossing over was studied in all four arms of the II and III, simultaneously, of future regular gametes, and of three arms of future exceptional gametes. Regional crossing over shown by regular gametes and the disjunctional arms of exceptional gametes differs little or not at all from the control. Crossing over in the non-disjunctional arm of exceptional gametes is either reduced slightly or does not differ from the control. The small crossover reduction in non-disjunctional arms of the two types of exceptional gametes is about the same. Therefore, since one type of exceptional gamete occurs with nearly twice the frequency of the other and since the rate of formation of the different kinds of gametes is the same in the male, where no crossing over occurs, as in the female, there appears to be no directive influence of crossing over upon disjunction in females of this heterozygous translocation.

SEARS, E. R., U. S. Department of Agriculture and University of Missouri, Columbia, Mo.: *Monosomes, trisomes, and segmental interchanges from a haploid of Triticum vulgare.*——A haploid plant of *Triticum vulgare* produced 13 viable seeds when pollinated by a diploid. Eleven of the 13 resulting plants showed abnormalities at meiosis, varying from a single univalent in some plants to two univalents, two trivalents, and a ring of four in another plant. Univalents are considered to have been monosomes, trivalents to have been trisomes, and rings of four to have been segmental-interchange complexes. Segmental interchanges are attributed to crossing over in the haploid between paired, partially homologous chromosomes, while monosomes and trisomes could have arisen through one or more of several different regulatory processes of haploid meiosis. Sixteen monosomes, 5 trisomes, and 2 segmental interchanges were present in the 11 aberrant plants. Some of these aberrations affected the morphology, color, size, or vigor of the plants, but others were without appreciable phenotypic effect. In the progeny of monosomics two nullosomics were obtained, of which one was fertile. A tetrasomic, which resulted from self-fertilization of a trisomic plant, was indistinguishable from normal. The use of chromosome aberrants obtained from haploids provides a new method of analyzing *T. vulgare* and possibly other polyploid plants.

SHULL, A. FRANKLIN, University of Michigan, Ann Arbor, Mich.: *Distribution of intermediate-winged aphids in the family and its bearing on the mode of their production.*——Previous work indicated that, as judged from the total number in the family, there is a negative correlation between the frequencies of winged and intermediate-winged individuals. This could be interpreted to mean that intermediates result chiefly from changed rates of production of a stimulative (or inhibiting) hormone. Apparent correlation might, however, follow from a high degree of correspondence in one part of the family and a moderate reversal of the relation in another part, which would ill fit the hypothesis named. It is found that most of the negative correlation indicated by the total numbers is due to the strong tendency for winged offspring to appear early in the family, at which time the frequency of intermediates has always been relatively low. Later in the family the proportion of intermediates frequently varies in the same direction as does the proportion of winged offspring, though this relation fluctuates greatly. The principal regularity in the frequency of intermediates is the fact that its peak, when there is one, occurs usually after the middle, sometimes at the middle, of the family. These facts are regarded as indicating that intermediate wings are caused, not chiefly by changes in the rate of production of a hormone, but to a general loss of precise control of the stimulative (or inhibiting) process. That is, it is due to a widening of the gap between the concentration which initiates development (or inhibition) and the concentration which insures complete development (or suppression).

SINNOTT, E. W., BLAKESLEE, A. F., and WARMKE, H. E., Columbia University, New York City, and Carnegie Institution of Washington, Cold Spring Harbor, N. Y.: *The effect of colchicine-induced polyploidy on fruit shape*

in cucurbits.——A number of diploid pure lines in both *Cucurbita pepo* and *Lagenaria vulgaris* were obtained in the tetraploid phase by treatment with colchicine. A considerable increase in cell size was found in most of the tetraploids but the fruit itself was not always larger. Fruit shape was very different in the two types, however, the tetraploids tending to be markedly wider and shorter than the diploids. Developmental studies show that this difference is usually established at the very beginning of the growth of the ovary. In several cases it also involves changes in relative dimensional growth rates in later development, so that the difference increases as the fruit enlarges. These shape differences are presumably related to no genic changes, but they are similar to others known to be caused by genes. Thus a type which is a "sphere" as diploid becomes converted, in tetraploid phase, to a flattened form much like the "disk" type, which as a diploid differs by a single gene from sphere. Evidently the mechanism of the genetic control of fruit shape is concerned with the number as well as the character of the genes involved.

SINNOTT, E. W., Columbia University, New York City: *Developmental factors affecting inherited differences in fruit size in cucurbits.*——By developmental analysis the size and the number of cells at various stages in the growth of fruits which differ markedly in size at maturity was determined. By daily growth measurements, differences between these fruits in the rate and the duration of their growth were also determined. Most size differences are related to differences in cell number and thus to the extent of cell division, but many involve considerable differences in the degree of cell enlargement. Rate of growth was found to be essentially the same in all size types, differences in size being dependent primarily on the duration of growth.

SMITH, HAROLD H., U. S. Department of Agriculture, Washington, D. C.: *Induction of polyploidy in Nicotiana species and species hybrids by treatment with colchicine.*——Seed treated with 0.2, 0.4, and 0.8 percent colchicine for 7, 10, and 14 days has produced double chromosome forms of *Nicotiana glauca*, *N. tabacum*, F_1 (*tabacum* × *glauca*), and a species hybrid segregant derived from crosses between *N. rustica* and *N. tabacum*. The induced allotetraploid from *tabacum* × *glauca* was fertile and made seed from which polyploid seedlings have been raised. Meristem treatment with 0.4 percent colchicine in water solution of lanolin paste has produced doubled chromosome forms of *N. rustica*, *N. glauca*, F_1 (*tabacum* × *sylvestris*), F_1 (*glutinosa* × *glauca*), and three species hybrid segregants derived from crosses between *N. rustica* and *N. tabacum*. Observations on the pollen showed that the hybrids had been made fertile by the treatment. Seeds and resultant seedlings have been obtained from the *tabacum* × *sylvestris* allotetraploid and the *rustica* × *tabacum* segregants. The induced autotetraploids of *N. rustica* and *N. tabacum* were more sterile and smaller with smaller, thicker leaves than the diploids. Two generations of polyploid plants have been grown from the original treated *rustica* diploids. Stomata of the polyploids of *N. rustica*, *N. tabacum*, *N. glauca*, F_1 (*tabacum* × *glauca*), and two *rustica* × *tabacum* segregants were found to

be about twice as large as in the undoubled forms. An increased number of chromosomes, indicating doubling, has been counted in root tip preparations of *N. glauca* (seedlings from treated seed), *N. rustica* (seedlings two generations removed from treated plant), and F_1 (*tabacum* × *glauca*) (seedlings from seed of allotetraploid).

SMITH, LUTHER, U. S. Department of Agriculture and University of Missouri, Columbia, Missouri: *Reciprocal translocations in Triticum monococcum.*——One naturally occurring and eighteen X-ray induced reciprocal translocations were studied. These translocations did not reduce fertility to the extent expected on analogy with the behavior found in maize. In a plant with a ring of four chromosomes only 11 percent of the pollen was empty and about the same proportion of florets was without seeds. In plants with no ring the sterility averaged 5.5 percent. Crosses among the interchanges resulted in associations of 6, 8, and 10 chromosomes and combinations of 4 plus 4, and 6 plus 4 chromosomes. In plants with a ring of six the sterility averaged 31 percent; with a ring of eight, 51 percent; with a ring of ten, 66 percent; with two rings of four, 24 percent; and with a ring of six plus a ring of four, 48 percent. Cytological observations showed that the segregation of chromosomes was directed at meiosis and that at first metaphase in at least 73 percent of the pollen mother cells (4,200 were observed) a ring of four presented a zigzag configuration. Nineteen percent of the cells had open rings and 8 percent could not be classified. The small discrepancy between the frequency of open rings and the degree of sterility can probably be accounted for by the apparent slight delay of disjunction in an open ring.

SPENCER, WARREN P., College of Wooster, Wooster, O.: *On the genetic structure of Drosophila hydei populations.*——*Drosophila hydei* populations near Azusa, California, Wooster, Ohio, and Gatlinburg, Tennessee all contain a large series of bobbed alleles. In extensive collections from Wooster populations of 1937 and 1938 from .25 percent to 1 percent of the males have been vermilion. Among over 12,000 males from Azusa vermilion was found only once. Wild flies containing sex-linked recessives include a scute male, a light male and a female heterozygous for a lethal from Azusa; a scute male and two females heterozygous respectively for cherry and garnet eye-color from Wooster. Several wild flies carrying autosomal dominants have been collected, including a male from Wooster with the dominant Gap vein and recessive grooveless in one 6th chromosome. Inbreeding tests of wild flies have yielded upwards of 100 new autosomals. Scarlet and carmine eye and abnormal abdomen are frequently recurring types. The third chromosomal gray body was recovered six times from the 1937 Wooster population, and not once from a much larger Azusa sample. From the examination of more than 50,000 wild flies and analysis through inbreeding of several hundred of these it may be concluded that: (a) a series of bobbed alleles is a character of wild hydei populations; (b) certain genes are frequent in one population and rare in another; (c) on the average approximately every other hydei female impregnated in

nature carries a visible autosomal of the order of phenotypic expression of the Drosophila mutants used at present in laboratory studies; (d) relative to the euchromatin involved, autosomals are more frequent than sex-linked mutants (bobbed excepted).

STILES, KARL A. Coe College, Cedar Rapids, Iowa: *The inheritance of brachymetapody.*——Brachymetapody in man is a condition in which certain digits of the hand or foot are abnormally short, due to the relative shortness of either the metacarpals or metatarsals. This rare condition has been reported as a dominant trait, but a study of a family in which the condition for genetical analysis of this trait were more favorable than usual gives strong evidence that it is certainly not regularly dominant. While brachymetapody appeared in individuals of this family who were heterozygous for the character, other members who were doubtless carriers of the defective gene, did not show the trait. This, then, constitutes a type of inheritance which has been generally classified as irregular dominance.

STONE, WILSON S., and GRIFFEN, ALLEN B. University of Texas, Austin: *Studies in chromosome conversion.*——(1) Conversion of part of the X to an autosome *Tl-4A*, w^{m5} is a reciprocal translocation involving exchange of the XL through the white locus (3C2, BRIDGES '19) for 4R through 101Fl; genetically the break is between eyeless and bent. Tl-4A, 18 w^{mA} is a reciprocal translocation with XL through the white locus (3C2) exchanged for the free end of 4L beyond the fifth heavy band (see GRIFFEN and STONE, these abstracts). A stock homozygous for *mA*, having no free fourth and consequently hyperploid in the male for XL, will live and is fertile. Further a stock homozygous for *m*5 XL and *mA* XR, with two normal free fourths and the males hyperploid for *m*5 XL is viable and fertile. As long as these stocks are carried in this condition (spontaneous non-disjunction may eliminate the hyperploidy of the male) a part of the X chromosome has been converted into an autosome, that is, it is not concerned in determining sex through a shift in dosage. In each case the part of the fourth exchanged now changes dosage with the chromosome mechanics of sex determination. These cases differ in that the first shift is accomplished by attaching the XL to a nearly complete autosome (the exchanged part is haplo-sufficient) whereas in the second case the XL became a "new" chromosome pair thereby increasing the chromosome numbers through the utilization of a free though reduplicated centromere.

(2) Conversion of a part of an autosome to the X chromosome. Tl-4A, 10 is a mutual translocation with XL through 1A6 (BRIDGES 1938 map) exchanged for 4L through 102A1 (BRIDGES 1935 map). A stock has been established homozygous in the female and hemizygous in the male for 4R XR, while 4L with the remainder of 4R (102A1 through centromere) plus XL is homozygous in both sexes. There is no free fourth chromosome present; and contrary to our previous opinion the small XL+4LR chromosome can be seen in metaphase in exceptionally good cytological preparations. In this case the small XL has become autosomal whereas the 4R moved to XR, which

comprises most of the fourth chromosome, has become part of the X-chromosome. This stock breeds true. All these cases, both in (1) and (2), which differ in degree rather than in kind, are the artificially produced equivalent of the X-autosome relations between *D. pseudoobscura* and *D. miranda.*

SUCHE, M. L., PARKER, D. R., BISHOP, M., and GRIFFEN, A. B., University of Texas. Austin, Tex.: *Reversal of lethal factors.*——Several lethal point mutations and several lethals with gene rearrangements have been reversed to a non-lethal condition by irradiation of the haploid sperm in *D. melanogaster.* Several *Pm* alleles (SUCHE and GRIFFEN) have lost their lethal effect both by changes from *Pm* to a normal allele and by changes from *Pm* to *brown.* These changes in phenotype have also occurred independently of the reversal of the lethal. Both point lethals and lethals with translocations involving the second and fourth chromosomes have been reversed to a non-lethal condition (PARKER). The dominant Glazed which accompanies an inversion in the second chromosome has reversed to a normal eye shape both together with and independent of the reversal of the lethal condition (BISHOP and GRIFFEN). Whatever is the nature of these lethal factors, they cannot be deficiencies, unless one is willing to make the most improbable assumption that irradiation can create anew a particular gene or genes. They therefore must be point mutations or position effects, not losses, and these types of lethal mutations are capable of renewing their normal activity.

SUTTON, EILEEN, Carnegie Institution of Washington, Cold Spring Harbor, N.Y.: *Trisomics in Pisum sativum derived from an interchange heterozygote.*—— In *Pisum sativum* numerical nondisjunction sometimes occurs in the meiotic association of four chromosomes in Hammarlund's interchange heterozygote (K-line×N-line). The gametes with an extra chromosome may contribute to the formation of viable offspring, which occur with a frequency of about 18 percent. The shortest of the four chromosomes is always the one which fails to disjoin from its neighbors, and the trisomic plants with an extra short chromosome are characterized by large bracts. Interchange heterozygotes which are also heterozygous for genes located in the short chromosome give abnormal ratios in the trisomic class of their offspring, and this provides a new method for establishing gene loci in addition to that of breeding the trisomics and obtaining trisomic ratios. (Work done at John Innes Horticultural Institution, London.)

WARMKE, H. E. and BLAKESLEE, A. F., Carnegie Institution of Washington, Department of Genetics, Cold Spring Harbor, N.Y. *Effect of polyploidy upon the sex mechanism in dioecious plants.*——The use of colchicine to produce tetraploids in dioecious plants has provided a new approach to the study of sex inheritance, chromosomal balance, and sex expression. In the species studied, sex expression appears to be unaltered by the mere doubling of chromosome number. Doubling has not induced hermaphrodites as is supposed to have been done in *Empetrum hermaphroditum.* Second generation tetra-

ploids are now available for study in 3 species.——*Cannabis sativa.* Of 32 second generation plants, 4 are strictly male, 28 strictly female and none intersexes. Chromosomes were counted at meiosis in males and in roottips in females. Chromosome association at meiotic metaphase is predominantly bivalent, with only 0–3 quadrivalents. The apparent deviation from the expected 1:1 ratio of males to females, and the absence of intersexes is tentatively explained by assuming that XXXX and XXXY individuals are females, that XXYY individuals are males, and that in tetraploid males, X usually associates with X and Y with Y to form two bivalents rather than a single quadrivalent. A single intersex is triploid and presumably XXY.——*Spinacia oleracea.* Ten tetraploids and 8 triploids were determined by root-tip counts 6 plants have flowered (2 male and 1 intersex in the tetraploids and the same in the triploids). The apparent difference in sex ratio from that in hemp may be significant.——*Lychnis dioica.* A large number of tetraploids and triploids are being studied cytologically. It should soon be possible to relate sex expression to the sex chromosomes, which are easily distinguished.

WHITE, ORLAND E. The Blandy Experimental Farm, University of Virginia, Charlottesville, Virginia: *Fasciation—its characteristics, distribution, origin, hereditability, relation to environment, and plant-world analogy to cancer.* ——Fasciation, as commonly defined, is a flattened or ribbon-like expansion of the main axis or axillary organs of a plant. Its presence often results in alterations in the arrangement of the foliar and floral structures, but its most striking characteristic is the increase in weight and volume of the plant's tissues as compared with normal types of the same strain. It may affect any part of the plant. It is not correlated with changes in chromosome number, though it may produce meiotic irregularities. Records of its occurrence in most vascular plant families are known. It occurs most often and strikingly in the Rosaceae, Onagraceae, Leguminosae, Cactaceae, Simarubaceae, and Compositae. It originates as gene mutations, or as the result of environmental effects, such as pressure, mutilation by insects, frosts, man, associated with alteration of food and water relations. Gene and environmental fasciations occur in the same species. Gene fasciated races centuries old occur in Pisum, Celosia, and of lesser age in Nicotiana, Oenothera and Zea, breeding true 100 percent. Environmental fasciations have been repeatedly produced experimentally and in some cases such fasciations have been propagated asexually. A gene fasciated race in *Nicotiana tabacum,* when crossed with non-fasciated strains, in some cases gives 1:2:1 F_2 ratios; in other different strains, very complicated results, showing striking effects of modifying factors, and giving rise to non-fasciated segregates which carry the fasciated genes.

WHITING, ANNA R., University of Pennsylvania, Philadelphia, Pa.: *Sensitivity to X-rays of stage in oögenesis of Habrobracon.*——Each ovary consists of two ovarioles. An ovariole has at its basal end in mature females a sac which may contain five eggs in late metaphase or early anaphase I in which they remain until laid. In the central part is a series of first oöcytes (15±)

alternating with groups of nurse cells and increasing in size and maturity posteriorly. The largest one only is in late prophase. The anterior end consists of a club-shaped mass of mitotically active oögonia (SPEICHER, B. R.). Maximum numbers in a mature female would be metaphase or anaphase I 20, late prophase 4, first oöcytes 56± and a large number of oögonia. When mature wild-type unmated females are X-rayed (2,500 r) and their successive eggs (haploid) collected, numbered and carefully cultured, the first 14–17 eggs (laid at normal rate) show no evidences of development. Later eggs may hatch but rate of oviposition falls below normal after the first day and becomes extremely low after the third. Adult progeny vary from 4 to 24, occasionally interspersed with eggs which begin development but do not hatch, or which shrivel, or with inviable larvae or pupae. When treated females are mated to untreated males the first eggs are not enabled to develop. Diffuse chromosomes in meiosis may therefore be less sensitive than condensed to X-rays. Cessation of oviposition is due to disruption of oögonial region following treatment.

WHITING, P. W., and ANDERSON, R. L., University of Pennsylvania, Philadelphia, Pa. and Johnson C. Smith University, Charlotte, N.C.: *Red, rd (eyes), a second non-autonomous locus in Habrobracon.*——Black (wild-type) color diffuses widely into lighter areas of eyes mosaic for orange (+-*o*) and for ivory (+-o^i) and in the latter case ivory areas show orange color also. Eyes mosaic for orange vs. ivory (*o*-o^i) show very limited diffusion of orange into ivory regions. Thirteen males from dahlia/ivory compound mothers, o^d/o^i had 17 mosaic eyes (o^d-o^i) with ivory areas clear except for very limited diffusion of purple or brown (dahlia) color and no orange visible. Of two males mosaic for red, one (839), mosaic for cantaloup also (*rd*=*c*), had left eye cantaloup dorsally, red ventrally; right eye cantaloup; the other (868), mosiac for carrot also (*rd*-wh^c), had left eye red with a few carrot facets, right eye carrot dorsally, red ventrally and ocelli with dense brown pigment (absent from ocelli of carrot or of red). While cantaloup or carrot regions had clear-cut margin, the "red" regions adjacent to the lighter autonomous colors were black which faded gradually into typical red. Five males (from *o/rd* mothers) were clearly mosaic for orange but dark areas of their six mosaic eyes appeared black. Some may have been mosaic for red also with red color masked by diffusion, as in *rd-o*, or with red color masked by orange, as in +-*rd.o*.

WITSCHI, E., and RILEY, GARDNER M. State University of Iowa, Iowa City, Iowa: *Effect of inbreeding and selection on the frequency of prostates in female rats.*——In female rats prostatic lobes occur relatively frequently. In wild rats (Iowa City dump) 34 percent (total 29) were found to have one or two lobes, while in the quite highly inbred Wistar albino rate the incidence was 29 percent (total 939). The fact that in two other laboratory strains of very different origin the frequencies were 69 and 9 percent suggested that every ordinary stock of rats might be a heterogeneous population with respect

to genetic factors determining prostate development. Experiments in selective breeding support this contention, since it has been possible, within one year, to develop a strain of Wistar rats in which 83 percent of all females possess prostates (total 307). This situation is a striking illustration of the fact that in sufficiently large groups inbreeding without selection does not tend to render a mixed stock more homogeneous. On the other hand, every new line which is started with very few individuals may, by haphazard, represent a distinct deviation from the original stock. This probably explains the case of the above mentioned two laboratory strains of which one had an unusually high, the other an extremely low frequency.

ABSTRACTS OF PAPERS PRESENTED AT THE 1938 SUMMER MEETING OF THE GENETICS SOCIETY OF AMERICA

OTTAWA, CANADA, JUNE 27–30, 1938

HOWARD, ALMA, National Research Council Fellow (Canada), Department of Genetics, McGill University, Montreal, Canada: *Chromosome behavior in relation to cancer susceptibility in mice.*——The discovery by HUSKINS and HEARNE that a correlation exists in inbred mouse lines between high frequency of mammary gland cancer in females and low frequency of chiasmata in the primary spermatocytes of males has been confirmed and substantiated by further work on the same and other strains. Chiasma counts on hybrids between high and low chiasma frequency lines have shown, however, that unlike cancer susceptibility as reported by LITTLE and others, chiasma frequency is not subject to "maternal inheritance." Nevertheless, it is influenced to some extent by the milk which the young mouse receives, and in this way its behavior resembles that of cancer susceptibility as reported by BITTNER.

HUSKINS, C. L. and WILSON, G. B., Department of Genetics, McGill University, Montreal, Canada: *The internal structure of Trillium chromosomes.*—— Measurements of chromonema length before and after spiralization and analyses of changes of direction of coiling have now been completed on seven samples of Trillium undergoing meiosis at diverse temperatures. The data render existing torsion theories of spiralization invalid and show that it is associated with elongation of the chromonema.

JOHNSON, L. P. V., MCLENNAN, H. A., and ARMSTRONG, J. M., Division of Forage Plants, Central Experimental Farm, Ottawa, Canada: *Fertility and morphological characters in Triticum-Agropyron hybrids.*——The Agropyron species *A. glaucum*, and *A. elongatum* may be readily crossed with tetraploid and hexaploid species of Triticum. F_1 plants from crosses involving *A. glaucum* are completely sterile (with one or two possible exceptions), while in crosses involving *A. elongatum* a fair proportion of the F_1 plants show low to moderate degrees of fertility. Observations upon the first three generations of *A. elongatum* hybrids strongly indicate that continued selection of highly

fertile segregates will quickly lead to the production of lines reasonably constant for high fertility.——Agropyron characters are dominant to a pronounced degree in F_1. Since the practical objective of the work is the production of a perennial, large-seeded, drought-resistant forage plant, some Agropyron characters, such as coarse, harsh-textured stems and leaves, and small seeds will be selected against; others, such as perennialism, extensive root system, general hardiness and vigor will be retained if possible.——Since this objective requires selection of types with stronger *Triticum* tendencies than are shown by the great bulk of F_2 segregates, backcrosses to the *Triticum* parents have been made to counterbalance Agropyron dominance and thereby increase the proportion of wheat-like segregates. Backcrossing of the sterile *A. glaucum* hybrids to *Triticum* gives in many cases highly-fertile, wheat-like types. The proportion of perennial segregates is much reduced in backcross populations. After the original backcross, succeeding generations are produced by selfing.

Love, R. M., Cereal Division, Central Experimental Farm, Ottawa, Canada: *Cytogenetics of vulgare-like derivatives of pentaploid wheat crosses.*—— Fifth, sixth and seventh generation plants from pentaploid wheat crosses were examined cytologically and morphologically in 1937. Crosses were: Marquis ×Iumillo, Iumillo×Hope, Iumillo×R. L. 729, and Marquillo×Iumillo. Of 336 *vulgare*-like plants examined in 50 lines, 12, 3, 27, 50, 98, 140 and 6 plants had 28, 38, 39, 40, 41, 42, and 43 chromosomes, respectively. The 28-chromosome plants were confined to two lines; and in five lines only did all the plants examined have 42 chromosomes.——No less than 15 percent of the plants exhibited evidences of rearrangements of chromosome segments. In order of frequency, the abnormalities at first meiotic division were: heteromorphic bivalent (14), trivalent (14), quadrivalent (10), ring univalent (8), fragmentation (3), two trivalents (1), and two quadrivalents (2). One out of every seven 42-chromosome plants had detectable chromosomal rearrangements.——Each plant was examined morphologically for 18 spike characters. In general, the 42-chromosome plants were the more *vulgare*-like. There were exceptions, however, and it is worthy of note that these occurred in some plants with rearrangements of chromosome segments.

Munro, S. S., Poultry Division, Central Experimental Farm, Ottawa, Canada: *Induced lateral size asymmetry in the fowl*——When totally exposed, side-on, to a sublethal X-ray dosage (1,100–1,400 r), three day old chicks subsequently exhibit a lateral growth differential in skeletal structures. The absolute difference increases with age and when epiphyseal ossification is completed the bird may be markedly unbalanced. The uniformity of the difference throughout all skeletal structures might suggest injury to a central control over the growth processes, possibly through lateral inequalities in impairment of the central nervous system. This explanation appears to be ruled out, however, by the fact that the side nearest the rays is the most retarded and by the fact that when the wings are crossed dorsally at time of exposure

asymmetry in wing size is reversed. It appears that direct injury to cellular constituents, brings about alterations in cellular metabolism, thus retarding the rate of development. Bearing in mind that the side of the chick nearest the X-ray tube receives an appreciably greater intensity of radiation, it would appear that there has been produced a corresponding difference in the degree of cellular injury on the two sides resulting in the observed lateral asymmetry.

PETO, F. H., National Research Council, Ottawa, Canada: *Chromosome doubling induced by temperature shocks in hybrid zygotes of Triticum vulgare pollinated with Agropyron glaucum.*——*A. glaucum* crosses readily with any of the tetraploid or hexaploid species of Triticum but the F_1 is self sterile. Lack of homology between parental genomes is undoubtedly one of the important factors limiting fertility and efforts have been made to overcome this by doubling the chromosome number. Temperature shocks of 42–44°C. for 20 minutes were applied to Marquis wheat zygotes with a portable apparatus 16–24 hours after self pollination. These treatments produced in 1936 a number of plants with double the usual chromosome number, while the same treatments applied to hybrid zygotes were unsuccessful. However, in 1937, alternating high and low temperature shocks induced chromosome doubling in at least one hybrid zygote from *T. vulgare* var. *Kharkov* pollinated by *A. glaucum*. Eighteen hours after pollination the plants were subjected to 12 hours alternating hot and cold treatments viz.; 3 hours at 36°F., 3 hours at 109°F., 3 hours at 36°F. and 3 hours at 109°F. The meiotic behavior and fertility of the resulting 84-chromosome plant has not yet been determined.

PETO, F. H., National Research Council, Ottawa, Canada: *Fertility and meiotic behavior in F_1 and F_2 generations of Triticum-Agropyron hybrids.*—— Some F_1 plants of crosses between *T. vulgare* (2n-42) and *A. elongatum* (2n-70) are moderately fertile, having on the average less than seven unpaired chromosomes, whereas the sterile plants usually have about twice that many. F_2 plants of varying degrees of fertility (0–53%) from the progeny of a single F_1 plant of *T. vulgare* var. *C.A.N. 1835×A. elongatum* are being studied cytologically. The chromosome number of ten typical F_2 plants examined to date ranges from 54 to 59; 6 having 56, 2 having 55, 1 having 54 and 1 having 59 chromosomes. This indicates that the chromosome number will stabilize at 56 instead of at either of the parental numbers of 42 or 70. The number of univalents present was less than six in all but one plant and no correlation was found between fertility and number of univalents. Consequently, failure of pairing is not the limiting factor in fertility of this generation. Translocations between partially non-homologous chromosomes with consequent irregularity of segregation of parts of chromosomes and the possible elimination from certain gametes of fragments or whole chromosomes during meiosis probably accounts for the range of fertility noted.

REED, S. C., Department of Genetics, McGill University, Montreal, Canada: *Determination of hair pigments in the mouse.*——Transplantation tech-

niques have provided information regarding the time of determination of the coat pattern "black-and-tan." This method has also been used to indicate the presence of some substance which will cause "non-waved" cells to produce "waved" hair. A further modification involving the use of the chorioallantoic graft has shown that the pigment inhibitor in White Leghorn fowls is either specific to White Leghorns or is not present in the allantoic blood stream.

SANDER, H. G. F., Department of Genetics, McGill University, Montreal, Canada: *Chromosome aberrations as the cause of fatuoid, steriloid and subfatuoid mutations in oats.*——Alterations of the normal balance between the C chromosomes and the rest of the complex give rise to fatuoid, steriloid, and subfatuoid mutations. The alterations are produced by deficiencies of various degrees in the C chromosome; these act genetically as multiple alleles.

ABSTRACTS OF PAPERS PRESENTED AT THE 1938 SUMMER MEETING OF THE GENETICS SOCIETY OF AMERICA MARINE BIOLOGICAL LABORATORY

WOODS HOLE, MASSACHUSETTS, SEPTEMBER 1–3, 1938

BEDICHEK, SARAH, North Texas Agricultural College, Arlington, Texas: *Sex balance in the progeny of triploid Drosophila.*——Males from eight X-IV translocation stocks were crossed to triploids with recessive markers, producing sterile intersexual "duplication intersexes" with a short fragment of the X plus two complete X's and three autosomes and weakly fertile hypotriploid females with longer X fragments plus 2X3A. Duplication intersexes bearing interior regions of the X in triplicate were studied by combining right and left hand fragments from two different translocations. Of eight duplication intersexes with very short sections, covering successively the entire X chromosome, in triplicate, none showed a marked shift in the female direction. Therefore a single primary sex gene can not exist capable of producing a functional female when represented three times with 3A regardless of the dosage of the remainder of the X chromosome. There was a graded shift toward femaleness in the phenotypic appearance of individuals with an X fragment plus 2X3A with increasingly longer fragments. Individuals were hypotriploid with either right or left hand section of two translocations (*t-lz* and *lz-v* breaks.) Furthermore, fertility of certain fragment plus 2X3A aneuploids begins before the last trace of intersexuality vanishes, since some hypotriploids with the right hand fragment of the *t-lz* and *lz-v* breaks possess very rudimentary sex combs. For this reason and the fact that shorter sections from the left than from the right hand region of the X chromosome plus 2X3A result in weakly functional females, we may conclude that the portion of the X to the left of the *t-lz* break seems a little more female potent in relation to its cytological length than the portion to the right of this break. A drop in temperature to 18°C. produces intersexuality in those individuals

carrying the right hand fragment of the *t-lz* break but does not alter the female appearance and function of hypotriploids bearing longer fragments These results make more plausible the multiple sex gene theory of DOBZHANSKY and SCHULTZ.

BLAKESLEE, A. F., and AVERY, A. G., Carnegie Institution of Washington, Cold Spring Harbor, N. Y.: *Induction of diploids from haploids by colchicine treatment.*——By spraying growing points of haploids of *Datura stramonium* with colchicine solutions, doubling of chromosome number has been brought about with abundant production of 2n flowers and 2n capsules resulting. Since there is only one chromosome of a kind in haploid Daturas, doubling the chromosome number gives rise to diploid races which are homozygous except for possible new mutations which have not been observed in tests of ten induced 2n capsules from treated haploids.——If methods for the induction of haploids from diploids which are being investigated are successful, a ready means would be available for securing homozygous 2n races from highly heterozygous material (such as species hybrids) by doubling the chromosome number of such induced haploids.

BOCHE, R. D., Carnegie Institution of Washington, Baltimore, Md.: *Hymenopteran parasitism of Drosophila.*——*Eucoila drosophilae* Kieffer (Figitidae) is a small hymenopteran which parasitizes various species of Drosophila. Oviposition is made into the young larvae of the first or second instar. The parasite egg throws off a gelatinous membrane within two minutes after being laid. This membrane persists during embryonic development, and its method of formation appears to be different from any known to the author among insects.——The larva hatches out of the enclosing membrane in two days, and lies free in the body cavity of the host larva. The host continues its development normally through pupation and histolysis; development of the imaginal disks is well underway when the parasite which has now become a grub begins the active destruction of tissue. After consuming the contents, the grub passes through a metamorphosis within the pupa case and emerges as an adult wasp. The total period of development thus occupies 18 to 20 days. The adult lives two weeks, hence the generations do not overlap.—— Not all species of Drosophila are suitable hosts for the parasite's development, some being absolutely immune. Susceptible and immune forms are found among species both closely and distantly related to *D. melanogaster*, which is itself completely susceptible. Within *D. melanogaster*, moreover, no immune strains could be found among numerous wild type and mutant forms tested. ——Evidence from the distribution of eggs among host larvae shows that oviposition is certainly not a random one and suggests that the female parasite is able to discriminate between parasitized and unparasitized hosts.

BUCHHOLZ, J. T., and BLAKESLEE, A. F., University of Illinois, Urbana, Ill. and Carnegie Institution of Washington, Cold Spring Harbor, N. Y.: *Direct demonstration in the male gametophyte of the result of crossing over in Datura.*——

The gene *sl-2* has been located in the 5·6 chromosome. It slows pollen-tube growth to nearly half the normal rate, but is nevertheless pollen transmissible through splicing of styles, so that homozygotes in the sporophyte generation were obtained. Two pollen abortion genes (*pa-2* and *pa-12*) are also located in the 5·6 chromosome. It was therefore possible to combine these *pa* genes (using the latter as females) into plants with formulas *sl-2/pa-2*, and *sl-2/pa-12*. The first yields gametophytes *pa-2*, *sl-2* from non-crossovers and (*sl-2 pa-2*) and (++) from crossovers. All pollen grains with *pa-2* abort so that only two classes, *sl-2* and (++) are viable. Preparations of pollen tube test-slides show a large group of short *sl-2* pollen tubes and a small group of (++) tubes (crossovers) which grow out as long as normal pollen tubes. The preparations show that the crossover value for *sl-2/pa-2* is very low (±1%), that for *sl-2/pa-12* is much higher. Plants of the formula *sl-2/pa-2* yield so few (++) pollen tubes that they may be used as pollen parents for the rearing of *sl-2* homozygotes or for any pollination in which it is desired to transmit this gene through the pollen. If these plants are used as females they give offspring that are carriers of *pa-2* if half the pollen is aborted, and carriers of *sl-2* if the pollen is good.

BUCK, JOHN B., Carnegie Institution of Washington, Baltimore, Md.: *Structure of living salivary gland chromosomes.*——Since the usual method of examining "living" salivary chromosomes by dissection under paraffin oil was found to be very unreliable, recourse was had to a technique by which the chromosomes were studied directly through the body wall of the living larva. From an examination of the larvae of Sciara, Drosophila, Simulium and Chironomus, the following tentative conclusions were drawn concerning the visible structure of normal living salivary gland chromosomes: (1) In all the species studied there is very little free fluid in the nucleus, i.e., the chromosomes (plus nucleolus and chromocenter, where present) fill, or nearly fill the nucleus. (2) The banding in Sciara and Drosophila is sparse and indistinct, that in Simulium and Chrionomus sharp, detailed and in some respects like that in fixed preparations. (3) In all of the forms most of the bands are either smooth and uniform or finely granular. Few or no vesiculated bands are seen. (4) In optical cross section, the chromosomes are round and have a dark margin and uniformly granular interior. (5) No longitudinal fibrillae ("striations," "chromonemata"), such as appear in acetocarmine preparations, are visible. (6) No pronounced foam or alveolar structure of the achromatic regions is visible.

BURKS, BARBARA S., Carnegie Institution of Washington: *A case of autosomal linkage in man: congenital tooth deficiency and hair color.*——The first clear case of autosomal linkage in man has been established through data in the family schedules of the Eugenics Record Office, and further corroborated through clinical study of families located in the field.——The "single-generation" method, or method of like and unlike sibling pairs, was used for detecting linkage between hair color and congenital tooth deficiency. Although the

mode of inheritance of neither trait had been clearly defined up to now, it was possible to use the linkage relationships between them to arrive at a reasonable hypothesis as to the genetic transmission of both traits. It was also possible to estimate their recombination ratio (approximately 14 percent), and to establish the genetic equivalence of missing third molars and other missing teeth, which had hitherto been thought to be independent traits.

CAROTHERS, E. ELEANOR, State University of Iowa, Iowa City, Ia.: *A hybrid Acridian gynandromorph.*——A species cross, *Trimertropis citrina* ♂ × *T. maritima* ♀, produced among more than 100 normal F_1 males and females one nearly perfect bilateral gynandromorph. Externally the left side was male and androgenetic; the right, female and a typical F_1 blend of the characteristics of the two species. The right halves of the ovipositor valves were fully developed and were opened and closed normally as maturity approached. The gynandromorph attracted males and also attempted to court females. Apparently, copulation was impossible structurally. Internally there was a right ovary with fully developed eggs and a normal right oviduct. No trace of either testis or ovary was found on the left side. Any explanation of the mechanism involved will have to take into consideration the following facts. 1. This is a half and half gynandromorph; therefore, whatever the mechanism, it became operative at the first cleavage. 2. The male half is androgenetic at least in regard to all pigment and pattern factors. 3. The female half is biparental. 4. The pigment and pattern factors are non-sex-linked as shown by reciprocal hybrids; therefore, the X chromosome in the male half could have come from either parent. 5. Parthenogenetically produced acridines restore the diploid number of chromosomes by means of an extra prophase split without cleavage (KING and SLIFER 1934) and are always females. If this gynandromorph was produced by chromosomal elimination one or more autosomes as well as an X were involved. It is highly questionably if such a cell would live and cleave. If dispermy is the explanation, and the diploid number was restored as in parthenogenesis, one X must have been eliminated or else the original one did not double when the autosomes did.

DOBZHANSKY, TH., and KOLLER, P. CH., California Institute of Technology, Pasadena, Cal., and Carnegie Institution of Washington, Cold Spring Harbor, N. Y.: *Sexual isolation between two species of Drosophila—a study on the origin of an isolating mechanism.*——Chiefly intraspecific, and only few interspecific, matings occur in mixed cultures containing equal numbers of females of *D. pseudoobscura* and *D. miranda* and of males of one of those species. After a 5 days exposure, approximately 95 percent of the females of the species to which the males belong, and less than 10 percent of the females of the other species, are impregnated. After a 21 days exposure, less than a quarter of the foreign females are fertilized.——The two races of *D. miranda*, coming from the Puget Sound region and from Mount Whitney respectively, show a preference for homogamic matings; this preference is much less pronounced than that observed in mixed cultures of *D. miranda* and *D. pseudoobscura*.——In cultures

containing females of only one species and males of the other a varying proportion of the females, but not more than 51 per cent, is fertilized after a 9 days exposure. If the *D. miranda* females used in such experiments belong to the Puget Sound race, the proportion fertilized depends upon the strain of *D. pseudoobscura* furnishing the males. With a single exception, strains of *D. pseudoobscura* from localities lying in or near to the area inhabited by the Puget Sound race of *D. miranda* give a lower frequency of fertilization than do strains coming from remote localities. No such result is obtained in experiments where the Whitney race of *D. miranda* is used. Thus, strains of *D. pseudoobscura* show not only genetic differences in their reactions toward *D. miranda*, but these reactions are not identical toward the two races of the latter species. It is concluded that genetic variability affecting the behavior of the flies in interspecific crosses is present within either of the two species studied. Such variability may furnish building blocks from which isolating mechanisms can develop.

Dove W. Franklin, University of Maine, Orono, Me.: *A study of individual versus group needs as a theoretical and an experimental approach to aggridascendance.*——From statistical analysis of the nutritional needs of all individuals of the group, the following observations have been made: 1. That preferences for foods are, in part, individual and, in part, group manifestations of nutritional needs. 2. That when the group is treated as an ever-shifting population of rated individuals, the optimum *group* manifestations of nutritional needs (for growth) are similar to those of the *individuals* who have been rated during the period of growth to lie between the mean and the maximum for rate of growth. Since this position in the group array represents an ever-shifting series of different individuals, a *type* is indicated. And, since the type is integrated from individual (*id*) likeness-differences of all individuals of the group (*aggregate*), the superior or leader type has been called the *aggridant* type—an individual type integrated from the group as a whole. 3. That the aggridant type predetermines, specifically, which satisfactants, which ratios, and which quantities of satisfactants are necessary for group superiority. By following the desires of the aggridant, we have uncovered new food combinations which produce a growth rate as much as 30 percent above standard. 4. That the theory of aggridascendance is applicable also to the satisfaction of needs in general: to the planning of food-production programs, for instance and to the analysis of needs inherent in the socioeconomic structure. One tangible common denominator derived from these experiments is expressed by the aggridant in a specialization-diversification ratio. This S-D pattern of the aggridant type is one of the principal clues to a controlled phenogenesis—to aggridascendance.

Eastlick, Herbert L., University of Missouri, Columbia, Mo.: *A study of pigmentation in the chick embryo by means of limb bud transplantation.*——It has been demonstrated by means of limb bud transplants made between 40 to 70 hour chick embryos that cells lying adjacent to the neural tube (presum-

ably neural crest cells) are responsible for pigmentation of the fowl. 1. Grafts made between pigmented donors and pigmented hosts of the same age illustrate this clearly, providing the grafts become attached to the mesenteries of the host. If the right limb bud of the donor is cut free at the edge of the neural tube and the left limb bud of the same donor is severed at the level of the intermediate cell mass, the former transplant develops pigmented plumage while the latter possesses white feathers. 2. Brown Leghorn grafts made to White Leghorn hosts develop colored plumage if the pigment forming cells are included but in the absence of such cells white plumage results. 3. White Leghorn grafts made to pigmented hosts show that all transplants which become attached to the mesenteries develop typical White Leghorn plumage; transplants attached to the body wall by a narrow bridge are intergrades, while well attached grafts are always intensely pigmented. Pigmentation of these grafts seemingly is due to the migration of neural crest cells from the host. The pigment forming cells apparently do not cross the mesenteries. If pigmentation were due to a diffusible substance, the grafts attached to the mesenteries should become colored. The results indicate that the inhibitor in the White Leghorn acts specifically within the pigment forming cell. The inhibitor apparently is unable to block pigment formation by foreign neural crest cells.

HUGHES, ROSCOE D., Medical College of Virginia, Richmond, Va.: *The chromosomes in the hybrid between Drosophila virilis virilis and Drosophila virilis americana Spencer.*——A study of the salivary gland chromosomes of the hybrid between *D. virilis virilis* and *D. virilis americana* reveals striking differences in the linear arrangement of the bands in the two sub-species. If we use *D. virilis virilis* as the standard for comparison, then the hybrid shows that there are major inversions in chromosomes 1, 2, 4 and 5. Chromosomes 3 and 6 are essentially similar. Pairing is typically loose except in chromosome 3. There is no evidence for interchange between non-homologous arms. There appear to be no large blocks of bands in either sub-species which do not have homologous regions in the other sub-species. Metaphase plates of larval ganglia cells also show striking differences. Both the male and the female of *D. virilis virilis* have five pairs of rod-shaped chromosomes and one pair of dots. In the *D. virilis americana* female there are two pairs of V-shaped chromosomes, one pair of rods, and one pair of dots. The male of this sub-species has three V-shaped chromosomes, four rods, and one pair of dots. Two of the rods in the male appear to form a pair corresponding to the one pair of rods in the female. The other two rods seem to pair with one of the V-shaped chromosomes, one with each arm. I am indebted to Dr. WARREN P. SPENCER for supplying the stocks of *D. virilis americana.*

JOLLOS, VICTOR, Madison, Wis.: *Further tests of the role of cosmic radiation in the production of mutations.*——The mutation rate of two pure inbred stocks of *Drosophila melanogaster* was tested following exposures to various frequencies of cosmic radiation. Exposures at an altitude of 14,000 feet under

18 mm. lead produced an increase in the mutation rate about 3.32 times that at Madison altitude without lead. Exposures at the high altitude without lead, and at Madison under lead, increased the mutation rate about 1.36 and 1.30 times respectively. The results are consistent in both stocks and in separate periods of exposure. But the increase in the mutation rate is statistically significant only following exposures at the high altitude under lead.——The frequencies of cosmic radiations in the exposures are estimated to be 15, 5–6 and 3 times respectively higher than those at Madison without lead.——The figures for the exposures at Madison without lead and at the high altitude under lead indicate that not more than 16.67 percent of the "spontaneous" mutations at Madison altitude could be related to the influence of cosmic radiation. A general formula of the quantitative relation between intensities of cosmic radiation and frequencies of mutation can be derived, under the assumption that the mutation rate increases in a straight line, in proportion to the increase in cosmic radiation frequencies.

The results of the other exposures agree with this assumption. But they are not yet conclusive.

The tests and calculations permit only a rough first approach to a determination of the quantitative relation between cosmic radiation intensities and frequencies of mutations. The basic figures in the calculations are not yet sufficiently reliable, either on the physical or on the biological side. Necessary improvements in the measurements are discussed.

JONES, DONALD F., Connecticut Agricultural Experiment Station, New Haven, Conn.: *Variable effect of the C locus in maize following translocation.*——The paired dark and colorless areas in the aleurone layer of the corn kernel are known to be the result of segmental shift. The usual result of increasing the number of *C* alleles is an increase in color whether this is brought about by germ cell recombination or somatic cell recombination. In a few cases it has been noted that a chromosomal shift in the *C* region produces a color lighter than normal instead of darker. Clear cases have been found of colorless areas paired with areas lighter than the surrounding normal cells. In a few cases of inter-chromosomal exchanges, involving both *C* and *Pr*, light areas adjoin colorless and red areas. Light areas may also adjoin colorless and dark areas. Evidently the relocated *C* region not only fails to function as usual but prevents the normal action of the other *C* allele. In this way it acts like a partial inhibitor of color. This is especially significant in view of the fact that one of the known alleles at or near the *C* locus is an inhibitor of aleurone color that is variable in its action in different lines.

KALISS, NATHAN, Columbia University, New York, N. Y.: *The expression of a short lethal deficiency in Drosophila melanogaster.*——Male *D. melanogaster* embryos, hemizygous for an X-chromosome with the terminal deficiency *260–2* develop to fully formed larvae which fail to hatch from the egg. Deficiency *260–2* (DEMEREC, D.I.S. 7:39) has at least four known loci missing: *chlorotic*, *lethal-J1*, *yellow*, and *achaete*. Live mutants, in contrast with normal animals of

comparable age, are characterized by the feebleness of their hatching movements, by the large accumulation of calcium carbonate concretions in the posterior pair of Malphighian tubules, by the irregular distribution of gas in the tracheal system, and by the inability of the animals to withstand dehydration. The pigmentation of their mouth armature and cuticular spines is "yellow-type" in color, in contrast to the darker pigmentation of wild-type animals of comparable age.——The mutants die within the egg membranes about 48 hours after oviposition (at 25°C.). When placed in an isotonic or hypotonic medium they may survive up to about 80 hours without further development. The increase in length of life is probably due to the prevention of dehydration which the mutants undergo on the usual food medium. Their histomorphology is indistinguishable from normals of comparable age.—— Death of the mutants can not be ascribed to the pathological condition of any specific organ. It must be ascribed to some physiological upset which is operative at about hatching time, since the development and differentiation of the mutant embryo proceeds normally up to this time.

KAUFMANN, B. P., Carnegie Institution of Washington, Cold Spring Harbor, N. Y.: *An X-ray induced "reversed repeat."*——Among the F_1 progeny of a male *Drosophila melanogaster* irradiated at 3,000 r, one individual showed an intercalary duplication in the left limb of the third chromosome arranged in the pattern of a reversed repeat (abcd*gfeef*ghijk). Assuming that twin strands were present at the time of reunion of the broken sections resulting from irradiation, origin of the duplication may be attributed to fusion of sister chromatids at the same level, thus

abcd | efg | hijk·
abcd | efg hijk·

giving abcd*gfeef*ghijk·, and probably another strand of the constitution abcdhijk·, whose fate remains conjectural. The union of sister chromatids in the manner here indicated offers a possible explanation of the origin in nature of such reversed repeats as occur in the chromosomes of Drosophila.

KIMBALL, RICHARD F., Johns Hopkins University, Baltimore, Md.: *A lag in the change of phenotype following a change of genotype in Paramecium aurelia.* ——In the ciliate protozoon, *Paramecium aurelia*, the mating type is known to change in definite ratios at endomixis. When a change occurred in genotype from Type II to Type I, some of the animals remained phenotypically Type II for a while as shown by the fact that animals of both types were found for a short time after endomixis. However, all the animals later became Type I whether they were descended from animals that, shortly after endomixis, were Type I or Type II. Therefore, all the animals in question were genetically Type I. It appears, then, that the presence of Type II individuals for a time after endomixis was due to a lag in the change of phenotype, not to a genetic difference. The rate of the change of phenotype differed both for different animals of the same line of descent and for different exendomictic lines. No

lag was found for the change from Type I to Type II, possibly because it was too short to be detected. These phenomena are of interest from the point of view of the interaction of the genes and cytoplasm and of the time of action of the genes.

KOLLER, P. C., California Institute of Technology, Pasadena, Cal., and Carnegie Institute of Washington, Cold Spring Harbor, N. Y.: *Chromosome variation in populations of Drosophila pseudoobscura from contiguous localities.*——Samples of populations were collected in seven different canyons in the Panamint Mountains (California). The relative frequencies of various gene arrangements in the third chromosome were studied using the salivary gland technique. Populations inhabiting separate canyons were found to differ from each other, in spite of the fact that migration of flies from canyon to canyon is apparently not prevented by any natural barriers. It follows that even a population occupying a continuous habitable territory may become differentiated into local subgroups. It is suggested that this differentiation may be brought about by random variations in the frequency of the component types.

LANDAUER, WALTER, Storrs Agricultural Experimental Station, Storrs, Conn.: *Types of cross-beak in fowl.*——1. Cross-beak as a common malformation of chicken embryos in association with eye defects; not hereditary; frequency influenced by environment. 2. Cross-beak in late homozygous Creeper embryos, more frequent in Japanese Bantams than in ordinary Creepers. 3. A hereditary form of cross-beak in which chicks are normal at hatching time, the beak becoming crossed between one and two months of age; not a single factor trait. 4. A hereditary form of cross-beak in which the chicks have a cross-beak at (and before) hatching, but of which a certain proportion develops a normal beak later; not a single factor trait. Crosses between birds with these two types of inherited cross-beak give exclusively normal offspring. 5. An inherited type of cross-beak in which the upper beak is short at hatching time, becoming crossed subsequently. No true-breeding individuals obtained of types 3 and 4, in spite of inbreeding. Many genetically cross-beaked birds probably have normal beaks. Embryonic mortality is not increased by the cross-beak trait (type 3), but post-hatching viability of chicks with cross-beak is much below normal. Common to all types of cross-beak (type 5 not studied) are structural abnormalities and asymmetries of the skull. The cross-beak is probably only a secondary symptom of these skull abnormalities. Among the non-hereditary cross-beak embryos with eye deformities crossing of the upper beak toward the left is much more frequent than the opposite type. The reverse is true for homozygous Creeper embryos and for the two types of hereditary cross-beak studied in this respect.

LOEHWING, W. F., University of Iowa, Iowa City, Ia.: *Physiological factors involved in differentiation of male and female parts of the angiosperm flower.*——Recent work by the author and others shows flower formation to be due to a specific florigenic inductor (hormone), produced in leaves, which are the loci

of photoperiodic perception, whence the florigen normally is transferred to adjacent buds causing inception of flower primordia therein. In some instances at least, the length of photoperiodic exposure requisite for functional megaspore formation is less than that for production of viable pollen. This fact underlies the frequent occurrence of pollen sterility of greenhouse plants in the winter. The usual peripheral position of staminate parts in the flower appears associated with higher oxidation potential at these points, due apparently to greater availability of oxygen and the stimulus of light. When light intensities are reduced, oxidation potentials in stamen loci fall and varying degrees of reversal in sex expression occur. Marked and highly localized nutritive differences distinguish regions of stamen and pistil formation. High sugar, phosphorus, phosphatase and oxidase characterize staminate and high nitrogen the pistillate zones. Data of the author indicate the importance of and necessity for micro-analysis on adjacent but often physiologically contrasted tissues. Normally there is no marked transfer of the flowering stimulus, but by certain combinations of exfloration and defoliation, evidence of transfer is demonstrable. Recent results suggest why earlier attempts to induce sex reversal by reciprocal grafts among staminate on pistillate plants of dioecious species were unsuccessful.

MARGOLIS, OTTO S., Western Reserve University, Cleveland, Ohio: *The effects of reduced atmospheric pressure and oxygen on facet number in bar-eyed Drosophila*——Data on the effects of reduced atmospheric pressure and of a pure oxygen atmosphere on the development of facets in Bar-eyed Drosophila are presented.——Flies which had spent varying portions of their egg-larval period (2 to 5 days) at one-half atmosphere pressure showed a very small, but for the most part statistically significant decrease in facet number. Exposures to reduced pressure all took place before the beginning of the temperature effective period.——Flies developed from larvae which had spent from the 24th hour of development to the 72nd hour in a pure oxygen atmosphere showed a very marked increase in facet number over the control group which developed under normal atmospheric conditions at 28°. A second group which had spent from the 48th hour of development to the 90th hour showed a somewhat smaller but significant increase in facet number.——It is concluded from these results that facet determining processes are in operation before the beginning of the temperature-effective period, i.e., about 50 hours at 28°; and that these can best be studied through the systematic use of new and controllable environmental variables such as the ones used here.

MARSHAK, ALFRED, The New England Deaconess Hospital, Boston, Mass.: *The stage of mitosis at which chromosomes are rendered less sensitive to X-rays by ammonia.*——When cells irradiated with X-rays are examined at various intervals after irradiation and the percent anaphases with unaltered chromosomes are plotted as a function of time after irradiation, a pronounced minimum is observed at three hours after irradiation. The cells in anaphase at three hours after irradiation were in the onset of prophase at the time of exposure

to X-rays. It was previously postulated that the marked sensitivity at this stage may be attributed to the appearance of positively charged surfaces upon the division of the chromonemata at this time. The hypothesis is supported by the observation that ammonia greatly reduces the sensitivity of chromosomes to X-rays. The theory further required that the onset of the prophase be the stage which was principally protected by ammonia. To test this seedlings of *Allium cepa* were treated with 0.0025 N NH_4OH and given 80 roentgens of X-rays. Counts of the percent normal anaphases from such seedlings showed a sharp maximum three hours after treatment in contradistinction to the minimum obtained from those treated only with X-rays. After five hours the curves obtained from both types of seedlings are identical, indicating that the sensitivity at the resting stage is not altered. These results, therefore, offer additional support to the above mentioned theory.

MATHER, KENNETH, John Innes Horticultural Institution, Merton, England: *Chiasma frequencies in trisomic maize.*——It has been shown previously that competition, or inter-chromosome interference, as judged by the negative correlation of chiasma frequencies, is due to there being an upper limit to the number of chiasmata which may be formed in a nucleus. The different bivalents compete for these chiasmata. Certain further considerations, notably the behavior of tetraploids, indicate that this upper limit is related to the number of chromosomes present. The more chromosomes in the nucleus, the higher is the limit to the number of chiasmata which may be formed. On this basis, the addition of an extra chromosome to a diploid showing competition should lead to (a) a decrease in the strength of the competition and (b) a corresponding increase in the mean number of chiasmata formed in the nucleus, because the extra chromosome will raise the limit without increase in the length paired at pachytene, i.e., the length of chromosome effective for chiasma formation. A study of maize trisomics, made available by the kindness of Drs. RHOADES and ANDERSON, has fully verified these conclusions. Five plants carrying an extra short arm of chromosome five show a definite decrease in the negative correlation as compared with five sister diploids, and also have a correspondingly increased frequency of chiasma formation. Less extensive data on other trisomic strains are in agreement with these results. We may, then, relate the upper limit to the number of chiasmata in the nucleus to the number of chromosomes present.

METZ, C. W., Department of Embryology, Carnegie Institution of Washington, Baltimore, Md.: *Structure of salivary gland chromosomes in Diptera.*——With accumulated evidence showing that a salivary gland chromosome is "solid," not a hollow cylinder, earlier views considering it made of spirally disposed chromonemata or "genonemes" around a central core have largely been abandoned. Observers still maintain, however, that numerous chromonemata *are visible* in these chromosomes. BAUER (on Chironomus) and PAINTER and GRIFFEN (on Simulium) give detailed accounts based on this view. It should be pointed out that these accounts do not agree as to the

nature of what are called chromonemata. In the writer's opinion, based on study of both these genera as well as Sciara and Drosophila, the so-called "chromonemata" here are different aspects of an essentially honeycomb or alveolar organization. (Whether there is an underlying *invisible* organization made up of chromonemata is another question.)——Evidence will be presented on this subject. Space merely permits mentioning a few points here. For example, according to our evidence "chromonemata" in Chironomus (1) form diagonal crisscross at all optical levels in side view, (2) regularly intersect at granules, (3) are often continuous diagonally across *both* chromosomes of a pair. These are properties of honeycomb, not discrete, sister threads confined to one chromosome. Simulium "chromonemata" interpretation apparently (1) is based on assumption considering as unit "chromomeres" droplets apparently made of material from two bands, one of which may be removed by deficiency, (2) disregards granules and "chromomeres" lying between the "chromonemata," (3) gives special significance to products of distortion.

METZ, C. W., Department of Embryology, Carnegie Institution of Washington, Baltimore, Md.: *Observations on the nature and significance of minute chromosomal differences in species hybrids and in ordinary wild strains of Sciara.*——Dobzhansky and Tan have noted two types of chromosome differences in salivary gland chromosomes in Drosophila species hybrids—large ones due to gross chromosome rearrangements (mainly inversions and translocations), and minute ones involving only one or a very few "bands." In Drosophila the former type appears to be relatively common and the latter rare, both in hybrids and within a species. In Sciara, however, the situation appears to be reversed. Extensive study of salivary gland chromosomes in three species has revealed no case of inversion and only two of translocation, including both irradiated and non-irradiated material. Likewise, none has yet been definitely identified in the species hybrids. Minute differences, however, are common, both in pure species and hybrids. Ordinary mutation rate, with or without irradiation, is relatively high in Drosophila and very low in Sciara. It seems probable that lack of mutation in Sciara is due to lack of inversions and translocations, and that this latter is in turn due to some general difference in chromosome constitution or behavior in the two genera.——This supports the view that most "mutations" are mechanical chromosome rearrangements. Characteristics of the minute chromosome differences lead to the hypothesis that small (mostly single band?) duplications, followed by qualitative gene changes provide a primary mechanism of evolution in Sciara.

METZ, C. W., Department of Embryology, Carnegie Institution of Washington. Baltimore, Md.: *A recurrent, spontaneous break in a salivary gland chromosome in Sciara.*——In one particular wild-type stock of *Sciara ocellaris*, numerous individuals exhibit in salivary gland nuclei a complete, transverse break in one member of chromosome pair *A*, at a definite locus about two-fifths the distance from end *l* (possibly the spindle fiber locus). A small deficiency may be involved. Break appears to be present in all salivary gland cells of an

affected individual, but no broken chromosome has been found in any of the numerous mitotic figures of ovarian cells examined in these individuals.—— Apparently the break occurs in salivary gland cells during ontogeny, in a regular manner. No case has been found in which both homologues are broken. The phenomenon or condition appears to be inherited, and preliminary data suggest that half the offspring from a pair mating show the effect. No such condition has been found in other stocks.——The case may have bearing on the problem of the mechanism of chromosome rearrangements. On the hypothesis that chromosome breaks precede rearrangements and that free, broken ends attract one another, it might be expected that union of the closely approximated free ends would occur here, but apparently such is not the case. It seems probable that the break is not mechanical, but is "autonomous," and that it occurs early in ontogeny. Conditions in other glands, etc., are being investigated.

POULSON, D. F., Yale University, New Haven, Conn.: *Polyploidy in eggs of Drosophila melanogaster carrying X-chromosome deficiencies.*——In zygotes deficient for the entire X-chromosome (nullo-X) development becomes abnormal through the failure of the regular distribution of nuclei to the surface and the subsequent failure of blastoderm formation. In eggs deficient for either the left or the right halves of the X-chromosome normal development ceases at slightly later stages. Of the cytological abnormalities common to these three deficient types, the most frequent and conspicuous are polyploid nuclei and multinucleate cells. These are usually found in nests and may lie in any region of the egg occupied by nuclei or cells. The nuclei may be tetraploid or of a higher degree of polyploidy. While the multinucleate cells most probably arise when cell division fails to keep step with nuclear division, there are two likely ways of obtaining the polyploid nuclei. The chromosomes may divide without the rest of the cell dividing and remain in the same nucleus; or, the nuclei may divide without the cell dividing and in the next division the spindles of the resulting multinucleate cell may fuse to give polyploid nuclei. The latter is very frequent in these eggs. Incomplete fusion of spindles may give multipolar spindles and abnormal distributions of chromosomes. If there is sufficient space the spindles do not interfere, and the number of nuclei increases. The behavior of the spindles is much the same in syncytial regions of the eggs where cell formation fails or is incomplete. The situation reported is very similar in many respects to that found in the testes of A/B hybrids of *D. pseudoobscura* (DOBZHANSKY).

PAYNE, NELLIE M., University of Minnesota, Minneapolis, Minn.: *The "yellow" colors in Microbracon hebetor (Say) [Habrobracon juglandis (Ashm.)].* ——There are at least three chemical groups of "yellow" eye colors in the adults of *Microbracon hebetor*, By "yellow" is meant any color in the range from white to red provided one of the pigments in the chemical series is yellow. The carrot, *wh*^{c}, eye contains carotinoids; the orange, *o*, flavones. A third group of eye "yellows" as yet unaffected by any genic change yields uric

acid on hydrolysis. The wild type eye contains pigments of all three types of yellow and in addition melanin which is related chemically to the proteins, is black and obscures the yellow pigments. White, *wh*, an allele of carrot is apparently due to absence of pigment. Ivory, o^1 of the orange series contains a reduced flavone which may become yellow when hydroxyl groups are added to it. The identity of the carotin in the carrot eye has been tested by removing it from the food of the host larvae. When this was done, carrot wasps had white eyes. Body color yellow is not identical with any of the eye yellows and is affected differently by culture temperatures.

RAFFEL, DANIEL: *A genetic analysis of apparent losses of the distal end of the scute-8 chromosome.*——When males containing the scute-8 chromosome, which contains an inversion the left break of which occurred between the loci of achaete and scute and the right break beyond bobbed and Block A in the chromocentral region, are irradiated, many cases of simultaneous yellow, achaete, and lethal mutations arise as was found by LEVIT, MULLER, PATTERSON and others. These cases were at first interpreted as losses of the distal ends of these chromosomes extending to the original point of breakage or extending to some point located in the chromocentral region that had been brought just to the right of the achaete locus. Investigation of several of these supposedly truncated X chromosomes by PROKOFYEVA showed that these left ends were present but indicated that minute rearrangements had occurred in them. The author carried out a genetic investigation to determine whether in all such cases the locus of lethal *J1*, the only lethal to the left of yellow of which a stock exists, was either lacking or affected. Males carrying lethal *J1* covered by the left end of scute-*J4* (a translocation to the third chromosome—in these flies the crossover suppressor CXF and Dichaete were present in the homologous third chromosome) were mated with females of 15 stocks containing yellow, achaete, and lethal mutations obtained by BELGOVSKY by irradiating sc^8 *B* W^a X chromosomes. In five of these fifteen crosses females with Bar and Dichaete were obtained. Here scute-*J4* was absent and lethal *J1* must have been "covered" by the X chromosome containing the yellow, achaete and lethal mutations. This demonstrates that in these five cases, at least, the simultaneous mutation of the yellow, achaete, and a lethal was not due to the loss of the left end of these chromosomes. It shows also that other lethal genes besides lethal *J1* lie to the left of achaete. And this, along with PROKOFYEVA'S cytological investigations, removes the last evidence for the survival of so-called simple breaks or the possibility of the existence of chromosomes lacking the terminal piece. Hence it supports the conception of the telomere or terminal gene as a permanent chromosome structure.

SAX, KARL, Harvard University, Cambridge, Mass.: *The effect of X-rays on chromosome structure.*——An analysis of irradiated microspores of Tradescantia has led to the following conclusions. (1) A single X-ray "hit" can break two adjacent sister chromatids. (2) Broken ends of sister chromatids invariably fuse to form a bridge and a U-shaped fragment at anaphase. No such

fusion occurs if the break occurs in the resting stage before the chromosome is split. (3) Induced breaks do not occur at random in the chromosome, a fact which indicates that secondary factors play some part in breakage. (4) There is no temperature coefficient for X-ray-induced aberrations. (5) The chromosomes are most susceptible to X-rays during prophase, and are more susceptible to breakage at meiosis than at mitosis. The differential susceptibility is attributed to mechanical factors. (6) Simple breaks are produced by single hits, but fusions between different chromosomes are caused by two independent hits. The relation between dosage and chromosome aberrations approaches a two hit curve,—breaks $= 1 - e^{an}(1 - an)$. The discrepancy between this curve and the mutation curve $(1 - e^{an})$ can be attributed to the fact that most of the visible chromosome abberrations are of the type which would not survive many cell generations. (7) Mutations produced by mechanical changes in the chromosome, induced by a single "hit," can be attributed to breaks in adjacent gyres of the chromonema leading to small inversions and deficiencies. (8) Few of the X-ray "hits" on the visible chromonema result in either chromosome aberrations or mutations.

SCHWEITZER, MORTON D., Cornell University Medical College and the New York Hospital, New York, N. Y.: *Role of heredity in childhood rheumatism.*——(This report is based on family studies made in the clinic of Dr. MAY G WILSON and was aided by a grant from the Commonwealth Fund.)——Making use of techniques for the application of genetic analyses to the features of human clinical material, the role of heredity was unequivocably verified. Confirmatory were the results with twins. Four pairs of identical twins were all affected, while among 12 fraternal pairs, 7 showed the disease in only one member.——Factorial analysis showed agreement with a single recessive gene hypothesis, the standard error being very small. Simple dominance, sex linkage, two or more recessive or dominant gene hypotheses were excluded. Comparable analyses of data from other laboratories gave concordant results. The penetrance (expression) of the disease in this material was quite high (82 percent), thus facilitating the analysis without the need for introducing statistical corrections.——The varying incidence in different communities and the marked paucity of cases among the children of people in favorable economic circumstances as compared with the usual clinic population is interpreted to mean that the presence of an hereditary susceptibility will not necessarily predestine every bearer to fall prey to childhood rheumatism. It is believed, rather, that definite environmental factors, general or specific are also required. This is consistent with the judgment of clinicians.——The verification of heredity as a dominant factor in the etiology of childhood rheumatism will make possible a reinvestigation of the various hypotheses regarding etiological agencies which have hitherto given equivocal results. It also provides a means of evaluating the efficacy of proposed preventive measures. Within a family where the disease occurs, it is now possible to assay the likelihood that a given child may fall victim to childhood rheumatism.

SINGLETON, W. RALPH, Connecticut Agricultural Experiment Station, New Haven and University of Missouri, Columbia: *Cytological observations on deficiencies produced by treating maize pollen with ultraviolet light.*——A recessive stock lg_1 gl_2 *b* v_4 was pollinated with dominant pollen, treated with filtered ultraviolet light. Pollen treatments were all made by Dr. L. J. STADLER. The filter used was the B filter of STADLER and SPRAGUE, P.N.A.S. **22**: 581. Of 1248 seedlings five showed recessive characters and were studied cytologically. Three (*lg gl b*) were haploids. One (v_4) had a heterozygous deficiency of 80 percent of the long arm of chromosome 2. The virescent character was accentuated over the normal condition. One was recessive for *b* initially but later developed fine streaks of sun red (possibly B). Progenies of this plant are being studied further.——In another experiment plants recessive for *a* were pollinated by dominant treated pollen using the same filter. Of 2,289 seedlings, 12 green ones (*a*) were sampled cytologically. Two were haploids. Three showed deficiencies for portions of the long arm of chromosome 3. One showed no deficiency.——In a third experiment pollen of the constitution *ABPl* was treated with the discharge tube giving nearly monochromatic radiation of 2,537 Ångström units. Sporocyte material was collected from 162 plants (the whole population) and stored in a refrigerator until pollen samples were examined. Plants showing segregating pollen were then examined cytologically Of the 162 plants, 31, or 19 percent, had segregating pollen. Diakinesis figures showed 10 pairs for all. One brown plant, *aBPl*, had a heterozygous deficiency involving 60 percent of the long arm of chromosome 3. Two plants showed no deficiency. One plant had a heterozygous deficiency for the short arm of chromosome 3. One had two heterozygous deficiencies, one on chromosome 4 and another on chromosome 8.——All heterozygous deficiencies so far observed were apparently terminal. No translocations were found

WARMKE, H. E., and BLAKESLEE, A. F., Carnegie Institution of Washington, Cold Spring Harbor, N. Y.: *Induction of tetraploidy in Nicotiana sanderae and in the sterile hybrid N. tabacum×N. glutinosa by colchicine treatment.*——From a series of plants of *N. sanderae* the seeds of which had been treated with different concentrations of colchicine (.2 to .8 percent), 35 have already flowered. Of these 18 (51 percent) have been found to be wholly or partially tetraploid as determined by pollen size. Seeds of the tetraploid flowers are distinctly larger than those from diploids. 4n corolla tubes are greatly enlarged. The second generation 2n and 4n offspring have been obtained and are being studied cytologically.——Seeds from the cross *N. tabacum*× *N. glutinosa* were supplied us by Dr. F. O. HOLMES. These hybrids were all sterile with ±98 percent aborted pollen grains. Growing points of the hybrids were sprayed with 1 percent colchicine in a lanolin emulsion, which has been found more effective than spraying with solutions. Characteristic roughening of leaves resulted in all cases. Of 39 plants, five (13 percent) have produced branches with different amounts (10 to 90 percent) of good pollen, and three have already set capsules with seeds following hand selfing. By colchicine treatment the chromosome number has been doubled, allowing the chromosomes of the

parental species to pair *intra se* The sterile hybrid has been transformed into a fertile allotetraploid.

WEINSTEIN, ALEXANDER, Zoological Laboratory, Columbia University, New York, N. Y.: *The arrangement of the chromatids in crossing over.*——The arrangement of the chromatids in the tetrad depends on the number of levels of crossing over, the distances between them, the number and nature of the exchanges at each level and their relation to exchanges at other levels (recurrence). These points have been tested by an analysis of all available data in *Drosophila melanogaster* and *D. virilis.*——Crossing over between sister chromatids is excluded because it would lead to negative frequencies of tetrads and, in attached X's, to values of homozygosis that are too low. Crossing over between more than two chromatids at a level would lower or eliminate homozygosis in attached X's. Recurrence must be random for the following reasons. (1) An excess of regressives over digressives would involve negative frequencies of tetrads. (2) An excess of digressives over regressives would lead to values of tetrad coincidence that are greater than 1 and to tetrad frequencies that are improbable or negative. (3) An excess of progressives would produce in attached X's too high a proportion of homozygosis and too low a proportion of individuals completely heterozygous; a deficiency of progressives would lead to deviations in the opposite directions.——These results make it possible to calculate in the tetrad the frequencies of internodes of various lengths and to determine on a genetic basis how the chromatids are arranged at and between levels of crossing over.

WHITE, M. J. D., University College, London, and Columbia University, New York: *A new type of anomalous meiosis.*——The general course of meiosis is remarkably similar for all organisms, the only animals with really anomalous meiosis falling into three groups; (1) animals with male haploidy, (2) some Scale Insects, (3) the male sex in many of the Diptera. Up till now the absence of crossing over in the male Drosophila and Sciara has been unparalleled elsewhere, the only other animals in which crossing over is entirely suppressed in one sex being those with haploid males. The present paper deals with the meiosis of some Mantids (Orthoptera) in which no chiasmata are formed in the male, and in which crossing over is presumably absent in that sex. The species dealt with are two: *Callimantis antillarum* Saussure (from the island of Haiti) and *Acontiothespis* sp. (from Yucatan). The first has eight pairs of autosomes, the second has only seven; both species are XO in the male. The usual diplotene and diakinesis stages are entirely absent in the male, and the first meiotic division is reductional for all parts of all chromosomes. Unfortunately the female meiosis is unknown up to now. Since in these Mantids there is no somatic pairing of homologous chromosomes, as in Drosophila, the existence of meiosis without formation of chiasmata raises some important points in connection with modern theories of meiosis.

WHITING, P. W., The University of Pennsylvania, Philadelphia, Pa.: *Sex-*

determination and reproductive economy in Habrobracon.—Theory of sex-determination proposed in 1933 was proved by sex-linkage for inbred stocks as shown in females (WHITING) and in males (BOSTIAN). In outcrosses sex-linkage is not obvious (DORDICK) and biparental males are replaced by females thus increasing reproductive economy in the species (WHITING). Various theories have been suggested to explain reproductive economy and failure of sex-linkage in outcrosses: differential maturation and chromosome breakage (WHITING), multiple factors (SNELL). At present a theory of multiple alleles appears best to fit the outcross pedigrees. None of these theories contradicts the principles of sex-determination as established for inbred stocks.

WOOLLEY, GEORGE W., Roscoe B. Jackson Memorial Laboratory, Bar Harbor, Me., and COLE, LEON J., University of Wisconsin, Madison, Wis.: *A new dwarf mutation (*dw_2*) in Rattus norvegicus.*——A second dwarf character in the rat differs in many respects (time of appearance, type of growth, reproductive ability, etc.) from the dwarf rat described by LAMBERT. Like the first described dwarf its expression depends upon the action of a monogenic recessive mutation.——The character may prove of value to the endocrine as well as the genetic field.——The mutation was first noted by one of us (WOOLLEY) in the genetics colony at the University of Wisconsin where study was started. Recently the mutation has been transferred to the Roscoe B. Jackson Memorial Laboratory for further study.

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